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Paleobotany and Paleoecology of the St. Mary River Spillway Locality (Late Campanian/Early Maastrichtian), Cardston, Alberta.

by

Michael Glen Riley ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Systematics and Evolution

Department of Biological Sciences

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Paleobotany and Paleoecology of the St. Mary River Spillway Locality (Late Campanian/Early Maastrichtian), Cardston, Alberta submitted by Michael Glen Riley in partial fulfillment of the requirements for the degree of Master of Science in Systematics and Evolution.

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Abstract

A study of paleobotany and paleoecology of the Upper Cretaceous (upper Campanian/lower Maastrichtian) St. Mary River locality has yielded a well-preserved compression/impression fossil flora that is composed primarily of aquatic plants inhabiting shallow lakes and ponds. Rapid deposition of overbank flood deposits preserved many plants *in situ*. Stratigraphy and depositional environments of the St. Mary River Formation are documented, providing a regional paleoenvironmental setting for the deposition of sediments and the preservation of the biota at this locality. A new genus and species of broad-leaved monocots similar to extant Limnocharitaceae (Alismatales) is described, and leaf venation is compared to that in living and fossil monocots. A systematic list of the flora shows that most taxa are floating or emergent aquatics and that at least three different genera at this locality show a floating rosette-forming habit. Preservation is remarkable with epidermal cell patterns, cuticular remains, and some internal anatomy present.

There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable.
There is another theory which states that this has already happened. ☺

Douglas Adams

Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveller, long I stood
And looked down one as far as I could
To where it bent in the undergrowth;

Then took the other, as just as fair,
And having perhaps the better claim,
Because it was grassy and wanted wear;
Though as for that the passing there
Had worn them really about the same,

And both that morning equally lay
In leaves no step had trodden black.
Oh, I kept the first for another day!
Yet knowing how way leads on to way,
I doubted if I should ever come back.

I shall be telling this with a sigh
Somewhere ages and ages hence:
Two roads diverged in a wood, and I -
I took the one less traveled by,
And that has made all the difference.

Robert Frost

The cloning of humans is on most of the lists of things to worry about from Science, along with behaviour control, genetic engineering, transplanted heads, computer poetry and the unrestrained growth of plastic flowers.

Lewis Thomas

Knowledge can be communicated, but wisdom cannot. A man can find it, he can live it, he can be filled and sustained by it, but he cannot utter or teach it.

Hermann Hesse

After silence, that which comes nearest to expressing the inexpressible is music.

Aldous Huxley

A vast radiant beach and a cool jeweled moon.
Couples naked race down by it's quiet side;
And we laugh like soft, mad children
Smug in the woolly cotton brains of infancy.
The music and voices are all around us.

Jim Morrison

Be what you would seem to be -- or, if you'd like it put more simply -- Never imagine yourself not to be otherwise than what it might appear to others that what you were or might have been was not otherwise than what you had been would have appeared to them to be otherwise.

Lewis Carroll

You can know the name of a bird in all the languages of the world, but when you're finished, you'll know absolutely nothing whatever about the bird... So let's look at the bird and see what it's doing -- that's what counts. I learned very early the difference between knowing the name of something and knowing something.

Richard Feynman

When you make the finding yourself - even if you're the last person on Earth to see the light - you'll never forget it.

Carl Sagan

For my parents,
Riordan and Gail Riley
and
for my wife,
Natalia

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Table of Contents

Chapter 1. Introduction

Introduction 1
Literature Cited 5

Chapter 2. Geology and Paleoenvironments of the St. Mary River Spillway

Location 10
Age 10
St. Mary River Formation Stratigraphy 12
Regional Paleogeography and Depositional Environments 14
Local Stratigraphy and Depositional Environment 21
  St. Mary River Spillway, site 1 23
  St. Mary River Spillway, site 2 26
  St. Mary River Spillway, site 2, column C 27
  St. Mary River Spillway, site 2, column B 30
Paleoclimate 35
Literature Cited 45

Chapter 3. *Cardstonia tolmanii* gen. et sp. nov. (Limnocharitaceae) from the Upper Cretaceous of Alberta, Canada

Introduction 70
Materials and Methods 71
Systematics 72
Results 73
  Russian Fossil *Haemanthophyllum* Leaves 75
  Extant Monocot Leaves 77
Discussion 85
  Comparison with fossil leaves 85
  Comparison with extant monocots 91
Acknowledgements 103
Literature Cited 104

Chapter 4. Conclusions

Conclusions 123

Appendix A Palynoflora - GSC Paleontological Report 6-ARS-1999 127
Appendix B Pie diagrams showing palynoflora abundance 135
Appendix C Correlation of beds from site 2, St. Mary River Spillway 136
Appendix D Leaf Margin Analysis 137

List of Tables

Chapter 2

Table 2.1 Systematics of flora from the St. Mary River Spillway fossil locality. 68

Chapter 3

Table 3.1 Comparative morphology of species of *Haemanthophyllum* Budantsev. 121

Table 3.2 Morphological comparison of *Cardstonia tolmanii* with selected extant taxa. 122

Appendix A

Table A St. Mary River Spillway: Palynology for selected sample sites. 134

List of Figures

Chapter 2

Figure 2.1 Map of Canada and aerial photo of St. Mary Reservoir locality. 58

Figure 2.2 Surficial geology of southwestern Alberta Foothills and Plains. 59

Figure 2.3 Geologic cross section through southwestern Alberta. 60

Figure 2.4 Correlation chart for the Campanian, Maastrichtian, and Paleocene. 61

Figure 2.5 Site 2 outcrop photomosaic and associated stratigraphic columns. 62

Figure 2.6 Photomosaic of outcrop from site 1.5 and site 2. 63

Figure 2.7 Photomosaic of outcrop from site 1 and site A-D. 64

Figure 2.8 Depositional structures and horizons from the locality. 65

Figure 2.9 Invertebrates from fossil locality. 66

Figure 2.10 Dinosaur, mammal teeth, and burrow traces from fossil locality. 67

Chapter 3

Figure 3.1 Map of Canada and aerial photo of St. Mary Reservoir locality. 110

Figure 3.2 *Cardstonia tolmanii* leaves from St. Mary River Spillway –1. 112

Figure 3.3 *Cardstonia tolmanii* leaves from St. Mary River Spillway –2. 114

Figure 3.4 *Haemanthophyllum* taxa from Russia. 116

Figure 3.5 Extant leaves of Alismatales: *Echinodorus*, *Caldesia*, & *Hydrocleys*. 118

Figure 3.6 Extant leaves of Limnocharitaceae: *Limnocharis* and *Butomopsis*. 120

Appendix B

Figure B.1 Pie diagrams showing relative abundance of palynoflora. 135

Appendix C

Figure C.1 Correlation of beds from site 2, St. Mary River Spillway locality. 136

List of Symbols and Abbreviations

Distance:

m	metre
μm	micrometre
mm	millimetre
km	kilometre

Latin words and abbreviations:

al.	alia (others)
cf.	confer (compare)
gen.	genus
nov.	novum (new)
sp.	species (singular)
spp.	species (plural)
incertae	uncertain
sedis	seat (affinity)
sensu	sense

Miscellaneous abbreviations:

Ma	Million years
pers. commun.	Personal communication
GSC	Geological Survey of Canada
SEM	Scanning Electron Microscopy
UALVP	University of Alberta Laboratory for Vertebrate Paleontology
UAPC-ALTA	University of Alberta Paleobotanical Collection

Legal description of location (Dominion Land Survey):

LSD	Legal Subdivision
Sec.	Section
Tp.	Township
Rg.	Range
W4M	West of Fourth Meridian
UTM	Universal Transverse Mercator System

Geologic abbreviations

K	Cretaceous Period
Kbo	Blood Reserve Formation
Kbp	Bearpaw Formation
Kb-s	Belly River/St. Mary River Formations
Kfm	Foremost Formation

Khc	Horseshoe Canyon Formation
Kmr	Milk River Formation
Ksm	St. Mary River
Ko	Oldman Formation
Kpa	Pakowki Formation
T	Tertiary Period
TKw	Willow Creek Formation
TKs	Scollard Formation
Tph	Porcupine Hills Formation

Lithologic Symbols

░	Sandstone
▒	Sandstone/Siltstone
┄	Siltstone
☐	Mudstone (shale)
▓	Bentonite layer
〰	Disconformity (erosional surface)

Chapter 1

Introduction

The St. Mary River Spillway fossil locality is located in southwestern Alberta, near the town of Cardston (see Fig. 2.1, 2.2). The productive fossiliferous beds at this locality are Late Cretaceous [late Campanian/early Maastrichtian (69-72 Ma)] in age (Harland et al., 1990; Hamblin, 1998b; Sweet, 1999) and part of the non-marine strata of the upper St. Mary River Formation (Nadon, 1991; Hamblin, 1998b; see Fig. 2.3, 2.4). More than 2,700 compression/impression specimens of predominantly fossil aquatic plants have been collected since 1993, when Shayne Tolman, a local teacher, brought the locality to the attention of Ruth Stockey.

North American geography for the Late Cretaceous puts southwestern Alberta at ~ 60° north paleolatitude, approximately 10° north of its present position (Smith et al., 1981; Sweet, 2001) with the interior of the continent flooded by the Western Interior epicontinental sea (Lerand, 1983). Paleoclimate estimates indicate ice-free poles (Spicer and Parrish, 1990), global mean annual temperatures 8-10° warmer than present (Wolfe and Upchurch, 1987; DeConto et al., 1998), and higher levels of O_2 and CO_2 (Berner, 1999; Beerling et al., 2002) resulting in vast mid- to high-latitude coal forming swamps and high latitude (85° north latitude) forests (Spicer and Parrish, 1990).

The St. Mary River Formation was first described by Dawson (1884). It is considered to have a lower brackish unit (30-60 m thick) characterized by abundant coal seams and oyster beds (Dawson, 1884; Lerand, 1983; Jerzykiewicz and Sweet, 1988; Nadon, 1991; Hamblin, 1998a, 1998b) and an upper freshwater unit (230-700 m thick) with rare coal seams (Williams, 1951; Nadon, 1994; Hamblin, 1998a). This upper unit contains abundant plant debris, gastropod and bivalve shell fragments (Nadon, 1988, 1991; see Fig. 2.9), dinosaur tracks, bones, and teeth (Langston, 1976; Currie et al., 1991; Nadon, 1993; Fig. 2.8d), and mammal teeth (Sloan and Russell, 1974; Langston, 1976; see Fig. 2.10). The upper unit is categorized as an anastomosed fluvial system consisting of repeating sequences of thin, discontinuous sheets of siltstone and shale interbedded with fine- to medium-grained sandstone and siltstone splay sheets and sandstone channel deposits (Nadon, 1991, 1994). A vast floodplain with numerous lakes and marshes and a peak in seasonal water flow characterize the depositional environment of the upper St. Mary River Formation (Nadon, 1994). The St. Mary River Spillway fossil sites also appear to represent a freshwater (Sweet, 1999) anastomosed fluvial system with channel deposits, shallow oxbow lakes and ponds, limited paleosol development and rare coal seams (see Figs. 2.5-2.8).

Bell (1949, 1965) originally described 18 species of compression/impression leaves from the St. Mary River Formation, but no collections from the St. Mary River exposures were reported. Later Stockey and Stockey (1993) reported on a low diversity fossil flora from the St. Mary River Spillway (site 1). This megaflora included an amphibious heterosporous fern, *Hydropteris pinnata* Rothwell et Stockey (1994) and large rosette-forming dicot, *Quereuxia angulata* (Newberry) Krysht. ex Baikovskaja (Stockey and Rothwell, 1997) both of which have been reconstructed as whole plants. An aquatic rosette-forming dicot, *Fortuna marsilioides* McIver et Basinger, an unknown herbaceous, chloranthoid toothed dicot, a sabaloid palm, and taxodiaceous foliage were also reported from this early site at the spillway. Further excavation revealed a more diverse flora (Riley and Stockey, 1999; see Table 2.1) with at least 32 species present. In this expanded flora, I have included a new genus and species of an emergent, broad leaved dicot, *Cardstonia tolmanii* Riley et Stockey (2003). A large rosette-forming, floating aquatic of unknown affinities has also been described (Riley and Stockey, 2000). Since fossil aquatic plants are rarely preserved in most floras, the locality promises to add much to our knowledge of Late Cretaceous aquatic plant reconstructions.

Plants from the St. Mary River Spillway flora have been compared to those in floras from the Late Cretaceous - Early Eocene deposits of western Kamchatka and the Koryak Highlands of eastern Russia (Budantsev, 1983; Golovneva, 1997, 2000). The aquatic plant communities in the late Maastrichtian-Danian deposits of the Koryak Highlands appear most similar to those from the St. Mary River Spillway (Golovneva, 2000). In Chapter 3, I provide details of a broad-leaved aquatic monocot, *Cardstonia tolmanii*, from the St. Mary River Spillway. The leaf shape, size, and venation pattern of *Cardstonia tolmanii* is compared to fossil leaves described as *Haemanthophyllum* Budantsev (Budantsev, 1983; Golovneva, 1987, 1997; Table 3.1) and with extant species from Alismataceae, Amaryllidaceae, Aponogetonaceae, Hydrocharitaceae, Limnocharitaceae, Stemonaceae, and Potamogetonaceae (Riley and Stockey, 2003).

Fossil plants from the St. Mary River Spillway locality are well-preserved as compression/impressions in siltstones and sandstones that were rapidly deposited in shallow freshwater lakes and ponds during overbank floods. As a result, many aquatic plants not normally preserved in the fossil record were buried *in situ*, enabling two whole plant reconstructions to date (Rothwell and Stockey, 1994; Stockey and Rothwell, 1997). The preservation is excellent in some aquatic leaves, where epidermal cell patterns can be traced over the entire leaf surface (Riley and Stockey, 2000). Other fossil leaves have cuticular remains and some stems and rhizomes show internal anatomy. Overall, such a well-preserved fossil aquatic plant assemblage is uncommon in the fossil record.

The purpose of this thesis is to first review the paleogeographic and paleoclimatic setting of the Late Cretaceous of North America and the northeastern Cordillera. A brief summary of the stratigraphy and depositional environments of the St. Mary River Formation is included, providing a global and regional paleoenvironmental setting for the deposition and preservation of sediments and the biota at the St. Mary River Spillway fossil locality (Chapter 2). A detailed description of the stratigraphy, interpretation of depositional environments, and a systematic list of the flora of the St. Mary River Spillway locality are also presented (Chapter 2). In Chapter 3, I present the description and systematics of a new genus and species of broad-leaved, emergent monocot, *Cardstonia tolmanii* Riley and Stockey.

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Chapter 2

Geology and Paleoenvironments of the St. Mary River Spillway

Location

The St. Mary River Spillway locality is 26 km northeast of the town of Cardston in southern Alberta, Canada (Figs. 2.1, 2.2). Fifteen designated fossiliferous sites are located on the north (sites 1-9) and south (sites 0, A-D) banks of the St. Mary River, downstream from the St. Mary Reservoir (Fig. 2.1). A detailed map showing all site positions is stored in the University of Alberta Paleobotanical Collections. Sites 1 and 2 have been extensively quarried and are the primary focus of this paleobotanical study (Fig. 2.1). Sites 0, 1, A-D are located on land belonging to the Province of Alberta, and sites 1.5-9 are on the Blood Indian Reserve.

The locality is located at 49° 2' North latitude and 113° 0' West longitude. The legal description of the area is SE1/4, Section 12, Township 5, Range 24, west of the 4th Meridian (Dominion Land Survey). The 1:50,000 topographic map of Raley 82H/6 (second edition map -1975) includes the fossil locality, the St. Mary Reservoir, and the nearest town, Spring Coulee. The Universal Transverse Mercator System (UTM) coordinates for site 1 are Zone 12U, 347300mE, 5470600mN (using North American Datum 1927). The fossil sites are above river level at elevations from 1045-1065 m.

Age

The St. Mary River Formation is Late Cretaceous in age and is considered age equivalent to the Horseshoe Canyon Formation with which it interfingers (Hamblin, 1998b; Fig. 2.4). If the base of the St. Mary River is broadly correlated to the base of the Horseshoe Canyon Formation and the contact with the Willow Creek Formation, then the St. Mary River sediments record approximately six million years, ranging from the latest Campanian to the late Maastrichtian (Harland et al., 1990; Lerbekmo and Braman, 2002; J. F. Lerbekmo, pers. commun., 2003; Fig. 2.4).

Based on seven samples taken near river level over a 700 m interval east of site 2 and from samples taken from drill cores used in the geotechnical study of the new spillway, the recovered palynomorph assemblages indicate an age of latest Campanian to early Maastrichtian (Sweet, 1999; A.R. Sweet, pers. commun., 2003; Appendix A). These age constraints are provided by *Aquilapollenites augustus* Srivastava and *A. drumhellerensis* Srivastava pollen (Catuneanu and Sweet, 1999; Srivastava, 1970; Sweet, 1999; Appendix A). The absence of *Scollardia trapaformis* Srivastava and *Mancicorpus gibbus* Srivastava pollen further constrains the age of the locality to the early early Maastrichtian (Catuneanu and Sweet, 1999; Lerbekmo and Braman, 2002; A.R. Sweet pers. commun., 2003; Fig. 2.4). In addition, the first appearance of *Pandaniidites* sp. is at the top of the Bearpaw that corresponds to an age of 72-72.5 Ma (Lerbekmo and Braman, 2002; A.R. Sweet, pers. commun., 2003). Art R. Sweet (pers. commun., 2003) used this palynomorph evidence to suggest that the fossil beds around the St. Mary River Spillway are 69-72 Ma in age.

The estimated age range of 69-72 Ma put the outcrop at or below the newly proposed Campanian-Maastrichtian boundary (Lerbekmo and Braman, 2002), which places it at or near the 31r-32n polarity boundary. Lerbekmo and Braman (2002) used magnetostratigraphic and biostratigraphic correlation (using miospores and ammonites) from sections in the Red Deer Valley and Cypress Hills of Alberta. The proposed 31r-32n polarity boundary by Lerbekmo and Braman (2002) corresponds to an age of about 70 Ma (Harland et al. 1990).

Drill cores taken by Agra et al. (1995) during the new spillway construction show a large portion of the stratigraphic section. However, the poor condition of the cores has yielded little palynological information to date (A.R. Sweet, pers. commun., 2003). It is possible that magnetostratigraphic and radiometric data may still be obtained, but the deteriorated condition of the cores could pose a problem (A.R. Sweet, pers. commun., 2003). Several kilograms of bentonitic material were collected from a thin layer overlying site 2 and within the fossil bearing strata near site 3 in the summer of 2002. The sample was sent to the Royal Tyrrell Museum for possible radiometric age dating. Currently, there are no radiometric dates or magnetostratigraphic zones available for the St. Mary River Formation. However, preliminary research (J.F. Lerbekmo, pers. commun.) indicates the top of the St. Mary River Formation might lie in the 30r polarity zone. This would place an upper limit of 66 Ma on the St. Mary River, which correlates closely to the top of the Horseshoe Canyon Formation (Lerbekmo and Braman, 2002; J.F. Lerbekmo, pers. commun., 2003; Fig. 2.4).

St. Mary River Formation Stratigraphy

The St. Mary River Formation, first described by Dawson (1884), is exposed in southwestern Alberta and northwestern Montana. Williams and Dyer (1930) interpreted Dawson's (1884) type section to be west of Magrath, Alberta, along the banks of St. Mary River. Later, Williams (1951) returned to this area to describe 354 m of the type section.

The formation generally increases in thickness to the west and varies from 230 m in the Plains to 950 m in the Foothills (Douglas, 1951; Williams, 1951; Irish, 1966; Rahmani and Schmidt, 1975; Nadon, 1988; Glass, 1990). However, overall thickness estimates are difficult to verify, due to the irregularity of dips in the Plains, and possible undetected thrusting in the Foothills and the Plains (Furnival, 1950; Nadon, 1988, 1991, 1994). Recent work indicates thicknesses closer to 650-700 m in the Foothills (Glen Stockmal, GSC, Calgary, pers. commun., 2003) and about 270 m along the St. Mary River near the spillway (Nadon, 1991). The formation has also been shown to be intertonguing with the Horseshoe Canyon Formation to the north, indicating contemporaneous deposition (Russell and Landes, 1940; Hamblin, 1998a, 1998b).

The St. Mary River Formation is generally considered to have two units. A lower, transitional, brackish water unit (bottom 30-60 m) and an upper, freshwater unit (Dawson, 1884; Lerand, 1983; Nadon, 1991; Hamblin, 1998c). The lower brackish unit is conformable with the underlying Blood Reserve Formation (shoreline/deltaic facies) and the overlying freshwater unit (Glass, 1990; Fig. 4). Abundant coal seams, carbonaceous mudstones, very fine- to fine-grained sandstones, oyster beds, and heavily burrowed, grey, gastropod rich siltstones characterize the lower unit (Jerzykiewicz and Sweet, 1988; Hamblin, 1998a). The upper freshwater unit comprises the majority of the formation and is described as an anastomosed fluvial system with an extensive floodplain (Nadon, 1994). It is characterized by discontinuous, thin sheets of interbedded very fine- to medium-grained sandstone, siltstone, and small amounts of carbonaceous shale to coal that surround medium- to fine-grained, lenticular sandstone lenses (Williams, 1951; Nadon, 1991; Hamblin 1998a). The sandstone lenses are 2-9 m thick and scattered throughout the formation. Lenses are less common than the thin sheets of sandstone and siltstone (Nadon, 1991). Sheets can be traced up to 1.5 km in some outcrops, are 0.1 m to 2 m thick, and thin rapidly from sandstone to siltstone away from lenses (Nadon, 1991). Detailed sections of the formation throughout the Plains and Foothills indicate a constant ratio of sandstone/(siltstone + shale). Roughly 34-38% of the formation is medium- to fine-grained sandstone and 62-66% is siltstone and shale (Nadon, 1991).

Due to both lateral and vertical heterogeneity of the St. Mary River Formation sediments, Nadon (1994) divided the formation into four facies associations: large sandstone lenses, small sandstone lenses, sandstone/siltstone sheets, and overbank fines. These facies represent channel and levee, splay-channel, crevasse-splay, and floodplain environments, respectively.

Bivalve and gastropod shells, invertebrate trace fossils, abundant plant material, and rooted horizons are seen throughout the formation (Nadon, 1988, 1991). Dinosaur bones, teeth, eggshells and tracks (Langston 1976; Currie et al., 1991; Nadon, 1993), turtle shells (Sloan and Russell, 1974), and mammal teeth (Sloan and Russell, 1974; Langston, 1976) are also preserved in the St. Mary River Formation.

Regional Paleogeography & Depositional Environments

North American geography and environments of deposition during the Campanian (83-70 Ma) and Maastrichtian (70-65 Ma) were significantly different than today. With higher sea levels globally (Haq et al., 1987), the interior of North America was flooded by the Western Interior epicontinental sea. This sea reached its maximum transgression during the Late Cretaceous, ~90 Ma (Turonian), and connected the present-day Gulf of Mexico to the Atlantic and Arctic Oceans (Lerand, 1983). By the late

Campanian, the epeiric sea had retreated slightly and the geographic position of North America was roughly 6-8° north and 20° east of its current latitude and longitude, respectively (Monger, 1989). The continent was rotated approximately 16° anticlockwise (Irving, 1983) with the North paleopole located near 74-78°N, 170-174°W (Irving and Irving, 1982; Marquis and Globerman, 1988). This places the paleopole near the northern tip of present-day Alaska. As a result, southwestern Alberta was positioned around 60° north paleolatitude (Smith et al., 1981; Sweet, 2001), 10° north of its present latitude. The Cordillera, a vast north to south series of mountain ranges on the West Coast, was uplifted high above sea level (Monger, 1989). The east coast bounded the inland sea with moderately elevated Appalachian Mountains, while the mid-continent Keewatin Highlands (north of present day Hudson Bay) split the sea to the north (Lerand, 1983).

Around 76 Ma (late Campanian), the seaway began one of its last major transgressive phases (Lerand, 1983). This event coincided with one of the early pulses of the Laramide orogeny (the latest and easternmost Cordilleran orogeny), and has lead some researchers to propose that thrust sheets and tectonic loading may have caused tectonic subsidence, contributing to the rapid advance of the sea (Shepheard and Hills, 1970; Nadon, 1988). In Alberta during this transgression, the sea reached as far westward as the northern and central Foothills. The marine shales deposited by the advancing epicontinental seaway during this period are referred to as the Bearpaw Formation (Alberta and Saskatchewan) and the Pierre Formation (North Dakota, Manitoba, and Montana) (Fig. 2.4). The sea then began regressing around 72.5 Ma (Braman and Lerbekmo, 2001). This regression is partly attributed to isostatic relaxation and uplift due to tectonic quiescence (Mack and Jerzykiewicz, 1989), but global changes in climate and geography may have also contributed (Spicer and Parrish, 1990). The increase in sediment supply due to tectonic quiescence and isostatic rebound (uplift) of the foreland basin (Heller et al., 1988), provided abundant clastic material for the progradation of nonmarine facies, namely the Blood Reserve, St. Mary River, and Horseshoe Canyon Formations in Alberta (Shepheard and Hills, 1970; Rahmani and Lerbekmo, 1975; Nadon, 1988). These advancing nonmarine sediments coincided with the retreat of the northeastern tip of the Bearpaw Sea into southeastern Alberta and southwestern Saskatchewan (Lerand, 1983).

The St. Mary River Formation sediments prograded in a north to northeast direction, coinciding with the overall northeast migration of the pre-Bearpaw, nonmarine, Oldman Formation, 78-74 Ma (Eberth and Hamblin, 1993). This contrasts with the east/southeastward progradation of the Horseshoe Canyon Formation and pre-Bearpaw, nonmarine Dinosaur Park Formation, 76-74 Ma (Eberth and Hamblin, 1993; Fig. 2.4). These data lead some researchers to suggest different source origins for each region. The St. Mary River and Oldman sediments originated in the eastern Cordillera of British Columbia and northwestern Montana, whereas the Horseshoe Canyon and Dinosaur Park clastics were transported from the northern and central regions of the Canadian Cordillera (Rahmani and Lerbekmo, 1975; Eberth and Hamblin, 1993). It is also suggested that a prevalent southeastward dip to the Alberta Basin existed, starting as early as the middle Cenomanian (Cant and Stockmal, 1989), but that it was not fully established until the late Campanian (Eberth and Hamblin, 1993). This southeasterly dip, parallel to the Cordillera thrust belt, appears to have persisted well into the Paleocene and controlled the overall southeastern dispersal of sediments in northern and central Alberta (Rahmani and Lerbekmo, 1975; Cant and Stockmal, 1989). However, regional variances in tectonic subsidence and isostatic rebound, slope, and/or clastic input may have accounted for the consistent N-NE direction of sediment dispersal and paleocurrent data seen in the Oldman and St. Mary River Formations in southwestern Alberta (Mack and Jerzykiewicz, 1989; Eberth and Hamblin, 1993; Nadon, 1994). In addition, the N-NE deposition of sediments in southwestern Alberta during the late Campanian to early Maastrichtian corresponds with the proposed Bearpaw Sea embayment in southwestern Alberta (Lerand, 1983). The proposed Blood Reserve/St. Mary River paleoshoreline was NE-SW oriented and presents an interface for the St. Mary River and Horseshoe Canyon Formations during regressive and transgressive phases of the Bearpaw Sea (Lerand, 1983).

In addition, sediment dispersal directions of St. Mary River and Horseshoe Canyon Formations correspond with the overall paleocurrent directions for the two formations of N-NE and S-SE, respectively (Rahmani and Lerbekmo, 1975; Nurkowski and Rahmani, 1984; Nadon, 1988; Hamblin 1998b). This suggests a transition zone where the St. Mary River drained into the southeasterly flowing Horseshoe Canyon Basin. Consequently, changing rates of uplift, subsidence and clastic input in north, central and southern regions of the Canadian Cordillera (Hamblin, 1998c; Eberth and Hamblin, 1993) may have caused the relative deposition rates and patterns to change over time, accounting for the interfingering of these two formations. North-south climate variability and minor seaway transgressions and regressions may have also accounted for or contributed to the interfingering (Jerzykiewicz and Sweet, 1988; Hamblin, 1998c).

The St. Mary River Formation sediments, which overlay the littoral Blood Reserve sandstones and marine Bearpaw shales, began to accumulate during the first major regressive phase of the Bearpaw Sea (Fig. 2.4). Aggradation of the St. Mary River strata appears to be continuous with no major unconformities. Although rates of sediment accumulation probably varied over the roughly six million years it took the formation to accumulate (Lerand, 1983; Nadon, 1988; J.F. Lerbekmo, pers. commun., 2003), they appear to average 100 m/1 Ma in the Foothills and 50 m/1 Ma in the Plains. Minor transgressions and regressions of the Bearpaw Sea, tectonic activity (uplift or thrust) or quiescence (isostatic rebound, relaxation), topography and climatic conditions probably contributed to variable sediment input and deposition rates (Lerand, 1983; Heller et al., 1988; Nadon, 1988; Hamblin, 1998). Yet, the overall clastic composition and input rate of the St. Mary River Formation appears to be quite stable over a long period of time. Nadon (1991) indicates that the sandstone/(siltstone + shale) ratios (0.51 to 0.60) show no statistical difference for measured basal, middle, and upper sections taken in the Foothills and the Plains. Stockmal et al. (1985) indicates that the evolution of a foreland basin in the area of a previous passive margin could have provided the observed composition of clastics seen in the St. Mary River Formation by the reworking of highstand system tracts of marine shales and siltstones, and shoreline and fluvial sediments.

Modern anastomosing rivers are characterized by numerous, sand-bedded, laterally stable, interconnected channels separated by topographic lows (Nadon, 1994). A seasonal peak in the water flow and an extremely low-gradient slope generate elevated, levee bound rivers with suspended loads that frequently inundate the floodplain with large amounts of sediment. The St. Mary River Formation sediments are also characterized by laterally stable and aggrading channel deposits that are associated with numerous, horizontally extensive sandstone/siltstone sheets and overbank fines. These sheets and overbank fines are generally found dipping below the levee, indicating that the floodplain was a topographic low (Nadon, 1994; Fig. 2.6b). Nadon (1994) estimates the paleoslope for the St. Mary River Formation to be around 10 cm/km (similar to modern anastomosed systems). This low angle slope was maintained over a 10,000 km^2 area for more than six million years, allowing for the aggradation of anastomosed fluvial deposits in southwestern Alberta (Nadon, 1994). Thus, the interpretation of the St. Mary River Formation by Nadon (1994) as an anastomosed fluvial system constrains the conditions and paleoclimate required for deposition.

The river channels of the St. Mary River Formation represent continual aggradation of sediments with little to no upward fining. This indicates that channel competence to transport medium-grained sandstones existed until total infilling, with little to no incisive action or downcutting (Nadon, 1994). The channel sandstones also show little lateral migration, but riverbanks had limited root structures to stabilize the levees. The buttressed floodplain deposits could have provided some lateral stability, however, levee deposits appear to have been reworked and frequently breached by the active channel. Consequently, levee breaches in the form of crevasse splays provided a mechanism that reduced flow rates in the active channel, thereby preventing river incision, causing the frequent anastomosing of channels seen in both modern and ancient systems (Nadon, 1994). As the sediments aggrade, the increased topographic relief of the channel from the floodplain created a gradient whereby the flow of the river is more efficient through a crevasse splay. As the splay channel enlarges, the active channel is gradually abandoned downstream (Nadon, 1994). This left a repeating pattern of numerous straight to sinusoidal sandstone lenses in the rock record of the St. Mary River Formation.

The floodplain environments of the formation are generally organic-rich siltstone and mudstones facies dominated by freshwater marsh and lacustrine environments (Nadon, 1988). Freshwater gastropod shells are common throughout the wetland marshes, but bivalves are relatively rare (Nadon, 1994). Beds of heavily burrowed sandstones are more common in the basal parts of overlying sandstone/siltstone crevasse-splay sheets (Nadon, 1994). Abundant poor to moderately developed soil horizons (paleosols) and rare coal seams with restricted lateral development are also present and frequently capped by siltstone deposits (Nadon, 1994). These sandstone/siltstone sheets are the result of seasonal floodwaters carrying abundant fine-grained clastics (Nadon, 1994). However, the thinness and rarity of coal horizons (Latour, 1961) and limited development of paleosols in the St. Mary River Formation are mostly due to a high input of fine-grained sediments onto the floodplain that interrupted soil formation (Kirshbaum and McCabe, 1992). In contrast, the Horseshoe Canyon Formation to the north has thick coal-rich horizons due in part to the low influx of sediment which allowed extensive peat swamps to develop and paleosols to mature over long periods of time (McCabe, 1984; Kirshbaum and McCabe, 1992). However, plant material was likely abundant during the wet season (Nadon, 1993), enough to support herds of large, nesting herbivorous dinosaurs during the non-migratory phase of rearing.

Locality Stratigraphy and Depositional Environment

Sedimentary rocks of the St. Mary River Formation that dip gently westward into the Alberta Syncline underlie the St. Mary Reservoir (Irish, 1966; Fig. 2.3). Folding in the area around the dam and spillway has resulted in strata dipping westward from 2.2° to 3.5°, at an azimuth of about 248° (Agra et al., 1995). Faulting near the dam is limited to a few small thrust faults with displacements of about 1 or 2 m (B. Rogers, Klohn-Crippen, pers. commun., 2000). A single fold, less than 4 m in height, was noted in outcrop near site 2 (Fig. 2.6b). It was noted that the Willow Creek Formation conformably overlies the St. Mary River Formation (in areas), but has been removed by erosion in the area around the reservoir (Irish, 1966; Fig. 2.3). This causes some difficulty in estimating the position of the fossiliferous beds around the spillway. However, previous work by Nadon (1991; pers. commun., 2003) indicates the exposed strata at the base of the spillway are in the upper 100 m of the formation along the St. Mary River, which is roughly 275 m thick. This would place the fossil sites in the upper freshwater unit of the formation. Palynomorph data also corroborate a freshwater environment (A.R. Sweet, pers. commun., 2003; Appendix A).

During the pre-construction phase of the new spillway in 1994, drill cores and geotechnical studies by Agra et al. (1995) document the strata from the top of the spillway (elevation 1110 m) to below river level (1010 m). Using local stratigraphic correlation, Agra et al. (1995) concluded that the 100 m sequence could be divided into five stratigraphic units. In ascending order, the sequences were labelled the Lower Mudstone, the Lower Interbedded Siltstone and Sandstone, the Massive Channel Sandstone, the Upper Interbedded Siltstone and Sandstone, and the Upper Mudstone

(Figs. 2.6b, 2.7a, 2.7b). Using these local stratigraphic units (Agra et al. 1995), the St. Mary River Spillway paleobotanical sites A to D and 0 to 4 fall within the Lower Siltstone and Sandstone unit whereas sites 5 to 9 correspond with the Upper Siltstone and Sandstone unit. Starting at river level, sites D, and 1 to 9 are higher in vertical succession, respectively. Sites D to A are also higher in vertical succession, respectively, but the correlation of the sediments seen at sites C, D and 0 with those seen in sites 1 to 9 is still uncertain.

Sites 1 and 2 are the principle fossil plant collecting localities to date, with the greatest overall diversity of taxa and total number of specimens coming from site 2. The total number of plant specimens collected to date for all sites at the St. Mary River Spillway is 2750. The invertebrate fauna discovered around the spillway consists of several gastropod taxa and one bivalve (Fig. 2.9). A small serrated theropod tooth from a carnivorous dinosaur (Fig. 2.10d) and the lower molar of a small marsupial (Fig. 2.10f) were discovered near site 4 and are currently housed in the UALVP collection under numbers 45699 and 45698, respectively. A ceratopsid cervical vertebra (D. Eberth, pers. commun., 2002; Fig. 2.10e) was photographed, but left *in situ* near site D.

The overall sandstone/(siltstone + shale) make up of the locality is similar to the ratios noted by Nadon (1991) for the entire formation, i.e., 0.51 to 0.60. The fossil bearing strata of the locality are also composed of all four facies associations that recur throughout the formation, and show both vertical and lateral heterogeneity (Nadon 1994): channel and levee sandstones (Figs. 2.6a, 2.6b, 2.7a, 2.8c), splay-channel sandstones (Fig. 2.6b), crevasse-splay sandstone and siltstone sheets (Figs. 2.6a, 2.6b, 2.8a, 2.8b), and floodplain siltstones and mudstones (Figs. 2.6a, 2.8a, 2.8d)

Many crevasse-splay and floodplain beds can be traced 10 to >200 m laterally in outcrop (Fig. 2.6b). The crevasse-splay sheets associated with channel sandstones generally extend 50 m or more laterally, and grade rapidly from sandstone to siltstone. This rapid lateral gradation is typical of a decreasing current, as the splay channel fanned outward upon entering the floodplain, depositing coarser sediments proximal to the main channel (Nadon, 1994). The lateral accretion and offset stacking of these sediments are indicative of the frequent, repeated, strongly seasonal flooding seen in modern anastomosed fluvial systems (Whitehouse, 1944; Nadon, 1994). The floodplain beds show greater variability in lateral range than crevasse-splay sheets, with beds rarely extending 100 m or more. Depositional environments also vary greatly, both laterally and vertically, in the floodplain of the St. Mary River Spillway.

St. Mary River Spillway, site 1

At site 1 (at the St. Mary River Spillway), grey and ripple laminated fine-grained sandstones alternate with pale yellow very fine- to fine-grained sandstones (Fig. 2.6b). Palynology indicates no marine or brackish influence to date, therefore, a freshwater environment is assumed (A.R. Sweet, pers. commun., 2003; Appendix A). The pale yellow sandstones are up to 1 m thick, appear to have mild limonite staining (A. Kimball, Univ. of Alberta, pers. commun., 2001), and are heavily burrowed with *Ophiomorpha*-like traces. The surficial burrow morphology shows scratch marks, pelletal reinforced sides, backfilling, and a knobby surface (T. Saunders, Univ. of Alberta, pers. commun., 2002; Figs. 2.10a, 2.10b, 2.10c). These traces are interpreted as a combined feeding and dwelling burrow (T. Saunders, pers. commun., 2002) Modern shallow marine (or brackish tolerant) shrimps such as *Calianassa* (ghost shrimp) show similar burrow morphology. However, studies of recovered *in situ* faunas from extant freshwater systems lead Hasiotis and Mitchell (1993) to conclude that paleoburrows with similar morphology could also belong to freshwater crayfish. In addition, the mildly oxidized sandstones and a climate with seasonal rainfall (Nadon, 1993) could indicate that the burrows were associated with drought tolerant freshwater crayfish. Burrow morphology of drought tolerant, freshwater crayfish such as the extant yabby (*Cherax*) from Australia, should be examined further for similarity to that seen in burrows from the St. Mary River Formation.

The intact shells of *Biomphalaria*-like gastropods (Hanley, 1976; P. Johnston, pers. commun., 2002; Fig. 2.9f) are also present, suggesting a large marsh or near-shore lacustrine setting (Hanley, 1976). In addition, the lack of roots or plant debris suggests a shallow, clear water, near-shore or shoreline lacustrine environment subject to seasonal flooding and periods of extremely high clastic input. An aggrading river channel with current directions N-NE underlies the burrowed beds (Fig. 2.7b). The channel developed a small levee initially and appears to have aggraded simultaneously with the burrowed layers. However, the levee does not appear to have aggraded once the sediments for the burrowed layers began to be deposited. This suggests that the channel remained competent, but that an increase in the local base level (raising of the water table) created a more deltaic setting. Oxidation of the successive burrowed layers from possible repeated aerial exposure might also indicate fluctuations in the local base level. The conformable and underlying Lower Mudstone unit observed in core (Agra et al., 1995), but not exposed in outcrop, could be interpreted as a large freshwater lake. A lake provides a local basin that would be affected by the annual and longterm increase or decrease in seasonal rainfall. This might provide an explanation for the local facies succession seen as repeated aggradation, then oxidation of near-shore or shoreline lacustrine sediments.

Site 1 appears to represent the basal portion of the Lower Siltstone and Sandstone unit. The site conformably overlies the proposed shoreline facies and appears to signal the return to a fluvial dominated environment with crevasse-splay and floodplain deposits. The base of site 1 is comprised of 1.5 m of siltstone deposits. The lower 1 m of siltstone is light grey in colour with little to no organic debris with rhizomes appearing near the top. The overlying 0.5 m of section is a dark to medium grey organic-rich siltstone with abundant leaves and rhizomes in the top 20 cm. The floating dicots, *Quereuxia angulata* (Newberry) Krysht. ex Baikovskaja and *Fortuna marsilioides* (Bell) McIver et Basinger, *Typha*-like monocot leaves, and the fronds or whole plants of the semi-aquatic heterosporous fern, *Hydropteris pinnata* Rothwell et Stockey, are the dominant flora of this section. The depositional setting is interpreted as a near-shore lake or pond in a floodplain environment. A 0.5-1.3 m thick, fine-grained, crevasse-splay sandstone unconformably overlies the siltstone unit. *Fortuna* rhizomes are abundant throughout the sandstone unit, whereas leaves of both *Fortuna* and *Quereuxia* are present in the basal portion. The sandstone unit is unconformably overlain by 0.6 m of a dark grey, organic-rich siltstone with degraded and fragmentary plant material. This unit is unconformably capped by a crevasse-splay sandstone, overlain by Quaternary glacial till. This is again interpreted as a near-shore lacustrine environment.

St. Mary River Spillway, site 2

Site 2 (Fig. 2.5) conformably overlies site 1 by 8-10 m vertically, but is offset by 420 m laterally. An underlying thick medium- to fine-grained sandstone bed (up to 1.5 m thick) with an irregular erosional upper surface or disconformity identifies site 2 in outcrop (Figs. 2.6a, 2.8c). Climbing ripples, parallel and cross-bedded lamination, trough cross-bedding, lag deposits with pebbles 1-1.5 cm in diameter, and offlapping sandstones are interpreted as structures associated with active channel and levee sandstones. Offlapping strata appear to be perpendicular to the NE flowing paleocurrent of the main channel, suggesting deposition by overbank flooding (Nadon, 1994). The basal contact is relatively sharp, flat and overlies crevasse-splay sandstones and siltstones.

Two vertical sections were measured at site 2: column A and column B (Fig. 2.5). Both columns were measured horizontally from a survey stake, just to the right of the photomosaic in Figure 2.5a. Column C and column B are 31 m and 99 m, respectively, from the survey marker. Column B is 68 m apart from column C. A prominent levee approximately 25- 35 m wide in outcrop separates the two columns (Fig. 2.5a) and appears to have created a slightly different depositional environment on either side of the levee. The bedding numbers (e.g., b-2b corresponds to a 0.3 m thick massive sandstone layer in column B of Figure 2.5) of both columns are correlated between columns and represent contemporaneously to simultaneously deposited sediments. Beds have been grouped into bedding sequences to represent similar facies associations or depositional environments (Appendix B, Fig B.1). If a genetically different bed was deposited on one side, but not the other, then a gap was left in the sequence to correlate the remaining strata. A description of the layers and an interpretation of the depositional setting for each column follows.

St. Mary River Spillway, site 2, column C

Starting at the base of column C and working to the top of the measured section, the basal sandstone contact, c-1, is relatively sharp and flat, but is also undulatory in areas. Lag deposits, cross-bedded ripples, parallel lamination and medium- to fine-grained sandstones indicate channel deposits with a flow direction of N to NE. Roots and rhizomes are rare. The contact unconformably overlies crevasse-splay sandstones and siltstones (not recorded in vertical column but visible to the left in section, Fig. 2.5a). The upper surface of the sandstone layer, b-1, is irregularly eroded and steeply incised (Fig. 2.8c). This may have resulted from the river avulsing upstream forming a new channel and/or from the reactivation of an abandoned channel. The levee deposits (Fig. 2.6a) appear to have remained intact but the active channel sediments appear to have been rapidly eroded, suggesting a reactivation of the old channel.

The basal contact of the new channel (c-3a) is erosional, with 0.3 to 0.4 m of siltstone-sandstone deposits with no sedimentary structure (and only a few fragmentary gastropod shells). One explanation for this unconformity could be the occurrence of a large flooding event, resulting in a temporary reopening of the abandoned channel, rapidly eroding and reworking the previous channel deposits. However, the absence of lag deposits, aggrading channel sandstones, and only one simultaneous offlapping levee deposit, indicate that the channel was rapidly abandoned. The upper surface of c-3a grades into the overlying brownish-black mudstone layer (c-3b).

Layer c-3b appears to represent a shallow lake or pond that was rich in organic content and very bioturbated (c-3b). The abundant, but mostly fragmented shells of the near-shore lacustrine (Hanley, 1976), bottom feeding (J. Hartman, pers. commun., 2003) *Lioplacodes* (Fig. 2.9c) and *Planorbis*-like (Figs. 2.9d, 2.9e) gastropods, indicate a clear water pond or lake environment (J. Hartman, pers. commun., 2003). The lake probably had emergent aquatic plants, that pulmonate invertebrates such as *Planorbis* could have used to crawl to the surface (J. Hartman, pers. commun., 2003). Taxodiaceous leaves and ovulate cones are rarely observed near the base of c-3b, but are found in greater numbers along with some fern fronds near the upper contact. In addition, the fining upward sequence increases in decomposed organic matter near the top, and the overall thickness of the layer (0.5 m) indicates that the lake evolved over time. The lake probably filled in over time and began to resemble a backswamp or lakeshore environment. An increase in taxodiaceous foliage and cones and the appearance of fern fronds are strong indicators of these types of environments. However, after the swamp or lakeshore environment began to develop, an erosional series of ripple-laminated, overbank grey to grey-green siltstones (c-4a) capped the lake.

The laminated siltstone layers, c-4a, with wave-rippled tops indicate a standing water floodplain setting that was frequently inundated with overbank deposits (Nadon 1994). Abundant, partially degraded but relatively intact leaves of aquatic or semi-aquatic plants are present in this siltstone layer. The floating or emergent leaves of *Quereuxia angulata*, *Fortuna marsilioides*, and *Cardstonia tolmanii* Riley et Stockey are occasionally preserved with vertically oriented stems in the successive siltstone layers. *Equisetum* L. stems and rhizomes are also common. These are interpreted as autochthonous deposits (Gastaldo et al., 1996, 1998). The occurrence of slightly decayed and abraded plant debris likely represents parautochthonous deposits from local lacustrine and levee taxa carried into the floodplain during overbank flooding (Gastaldo et al., 1996, 1998). Large *Typha*-like monocot leaves, taxodiaceous foliage, and cones are common components of these parautochthonous deposits. The siltstone layer, c-4a, is erosionally overlain by alternating massive fine-grained sandstones and thin ripple-laminated siltstones (c-4b).

Three-dimensional root and rhizome networks penetrate layer c-4b. Tubers and rhizomes similar to *Equisetum* are observed throughout the layer, indicating colonization by riparian and riverbank species (Fig.2.8b). The occasional intact shell of the sandy-bottom inhabiting gastropod *Viviparus* sp. (Pennak, 1989; Fig. 2.9a. 2.9b) indicates a clear water, fluvial or lacustrine setting (J. Hartman, pers. commun., 2003). The basal segment of the sandstone lenses in c-4b contain taxa found in layer c-4a. These are interpreted as autochthonous and parautochthonous deposits whereas the upper portion of the sandstone sheets contain highly abraded leaves and twigs from conifer, monocot and rare angiosperm taxa. These are interpreted as parautochthonous and allochthonous deposits swept in from upstream levee, lakeshore, and backswamp environments during major flooding events and levee breaches.

A thin, highly organic, brownish-black mudstone layer, c-5, with numerous shell fragments similar to the lower mudstone layer, c-3b, developed over the sandstone. This represents a return to a quiet lacustrine environment. The mudstone layer, c-5, is erosionally overlain by ripple laminated siltstones deposits (c-6a) similar in colour and texture to c-4a. The siltstone layer, c-6a, in turn, was capped by a series of massive sandstones (c-6b) with abundant root and three dimensional rhizome networks (Fig. 2.8b) throughout. Again, these represent crevasse splay deposits and show similar taxa to siltstone layer c-4b. The upper section of the column (c-?) was not recorded due to overburden obscuring the strata. The beds can be traced visually in outcrop from column B to column C and indicate that the missing upper section correlates with strata b-7a through to b-10.

St. Mary River Spillway, site 2, column B

Since the majority of the beds for column B and C are directly correlated, only differences in layers or depositional setting will be discussed here. The basal sandstone unit, b-1, is a massive levee sandstone possibly associated with the earliest flooding events of the 'old' river channel. A ripple-topped siltstone unit that fines upward (b-2a) erosionally overlies the basal sandstone. The siltstone unit (b-2a) shows little to no structure or organic debris. The basal portion of the siltstone layer, b-2, is comprised of siltstone/sandstone sediments that were probably the result of a reworking of the lower sandstone unit during a flooding event. The siltstone layer, b-2b, is erosionally overlain by fine-grained crevasse-splay sandstones that are cross-bedded to massive. Neither unit correlates with column C, but these are interpreted here to represent a series of flooding events prior to the incision and reactivation of the old channel in column C. The flooding event(s) that reactivated the adjacent channel (c-3a), appear to have eroded the top of the sandstone layer, b-2b. Therefore, layers b-3a and c-3a are interpreted as simultaneous deposits. The flooding events were apparently large enough to have eroded small channels into the upper surface of the levee sandstones (Fig. 2.5a, regions above X's). These incised channels filled with siltstone/sandstone sediments similar in composition and flora to b-3a and c-3b. This created a new levee environment which continued to separate the low-lying floodplain to the left (column B area) and the newly formed (incised) lake to the right (column C area). *Equisetum* rhizomes and roots are present near the peak of the levee sandstones whereas shoreline taxa (*Hydropteris pinnata*, *Onoclea*-like fern fronds, and angiosperm leaves), followed by near-shore taxa (*Quereuxia angulata*, *Fortuna marsilioides*, *Cardstonia tolmanii, Typha*-like monocot leaves) become common in the thickening mudstone and siltstone layers down-slope. The steep banks on either side can be traced in outcrop by following the profile of the organic-rich layers (b-5 and c-5).

The organic-rich mudstone layer, b-3b, and rooted siltstone bed, b-4a, correlate with c-3b and c-4a and appear to represent a shallow lake or pond that was capped by an overbank flood. The overlying, erosional sandstone/siltstone layer, b-4b, represents a series of crevasse-splay deposits concurrent with layer c-4b. This layer is heavily rooted with rhizomes, some twigs and assorted leaves. The gradational upward fining, organic rich mudstone layer, b-5, appears to correlate with the mudstone layer, c-5, suggesting the reestablishment of a shallow lake or pond environment. However, b-5 has two gradational but more or less distinct horizons. The lower horizon is light yellow to light brown in colour, lacks any structure, fractures in block-like pieces, and has a higher sand and mineral content than the upper horizon. The upper horizon is brown to brownish black, relatively thin, and high in organic content, particularly fusinite (Appendix A, P4454-2). These two zones could represent the A and B horizons of a moderately developed, periodically exposed paleosol (Retallack, 1988; Nadon, 1994). Palynomorph data recovered from a sample taken near the top of the layer suggest a near-shore lacustrine setting dominated by angiosperm pollen (Appendix A, P4454-2). The lacustrine interpretation is based on the abundance of the *Typha*-like pollen, *Sparganiaceaepollenites* and the occurrence of the tricolpate pollen, *Penetetrapites inconspicuus* Sweet. Large flat-bottomed indentations resulting from soft sediment deformation are occasionally visible in the upper mudstone layer (Fig. 2.8d). These are interpreted as tracks made by large herbivorous dinosaurs as they grazed or migrated in breeding season through the wetland areas (Nadon, 1993).

Section b-6, is a thick, ripple laminated greenish-grey to dark grey siltstone layer that correlates with the siltstone and sandstone layers, c-6a and c-6b. The siltstone layer, b-6, is slightly distal to the splay channel sandstones in the same layer to the right, representing an outward-fining sequence (Fig. 2.5a). This rapid fining outward sequence of sediments is typical of splay deposits as the flow rate rapidly decreases upon entering the floodplain (Nadon, 1994). Plant remains are abundant throughout this layer, especially in the laminated horizons. This is the most productive and taxonomically diverse layer for fossil plants at site 2. Fern fronds, taxodiaceous foliage, *Ginkgo*, strap-shaped and broad bladed monocot leaves, and entire and toothed margined dicot leaves along with various seeds, roots and rhizomes are present throughout this layer (Table 2.1).

Layer b-7a represents a lacustrine, organic-rich mudstone that is conformably overlain by a coarse-grained volcanic ash layer, b-7b. The ash layer, in turn, is erosionally capped by dark grey, floodplain siltstones, b-8, rich in plant leaves and roots. A brownish-black, lacustrine mudstone is reestablished, b-9, that too is erosionally overtopped by a series of massive sandstone sediments, b-10, that have abundant roots and other plant remains.

Tracing section b-10 roughly 20 m to the left of column B in outcrop (Fig. 2.5, far left edge of photo) reveals a heavily burrowed area with *Ophiomorpha*-like traces (Figs. 2.10a, 2.10b, 2.10c). The burrows are in the bottom 0.1- 0.3 m of crevasse-splay sandstones and appear to be identical to the *Ophiomorpha*-like traces from site 1 (Fig. 2.7b). Nadon (1993) indicated that similar traces are common occurrences throughout the formation in crevasse-splay sandstones. These burrows appear to be closely tied to oxidized floodplain sandstone deposits in near-shore lacustrine settings.

No coal horizons were noted at site 1 or 2, but one of the few coal seams recorded at the spillway is near site 4 (Fig. 2.8e). The seam is 2-3 cm thick and stretches for 30-40 m. The limited thickness and extent of the few coal seams observed is consistent with the rarity of coal horizons throughout the St. Mary River Formation (Nadon, 1991). McCabe (1984) indicated that lack of coal formation is closely tied to the level of clastic input; the higher the clastic input the lower the probability of coal formation. Smith (1986) showed that modern anastomosed systems rarely have coal present.

Overall, site 2 represents three of the four facies associations described by Nadon (1994): channel and levee, crevasse splay, and floodplain environments. The randomly occurring and alternating siltstone, sandstone, and mudstone layers indicate an environment prone to periods of strong seasonal flooding with a floodplain that was repeatedly inundated by overbank siltstones and/or sandstone/siltstone deposits. Rare coal horizons and the repeated interruption of soil formation by floodplain deposits indicate high clastic input (Kirshbaum and McCabe, 1992; Nadon, 1994).

Major flooding events, locally, appear to be followed by periods of low sediment deposition that allowed pond and lake environments to evolve free from high clastic input for long periods of time. For instance, the repeated succession of thinly laminated sediments with *in situ* leaves of aquatic and/or semi-aquatic plants and upward growing rhizomes indicate more frequent, possibly yearly, flooding events of a lesser extent or force. These siltstone layers and possible paleosols rarely reach 0.5 m in thickness before being capped by sandstone/siltstone splay sheets at site 2. This recurring pattern of siltstone/sandstone layering is seen throughout the locality, although the thickness of the siltstone layers can vary from less than 0.1m to > 2m locally. These recurring sequences are interpreted as a floodplain environment that was repeatedly inundated with silty floodwaters from minor flooding events at which time larger more catastrophic floods buried or entombed part or all of the surrounding floodplain with large volumes of clastic material. It has further been proposed by Nadon (1993), that the abundance of organic debris throughout the floodplain facies and the interpretation that large herbivorous dinosaurs nested in the area support the idea that a vegetatively lush, seasonal wetland persisted from year to year. Therefore, vegetative productivity was assumed to be high enough throughout the upper part of the formation to support these large dinosaurs over the duration of time it took to nest and rear their young (Nadon, 1993).

Overall, the regularity and frequency with which overbank fines and crevasse-splay sheets appear in the strata of the St. Mary River Spillway and the upper St. Mary River Formation indicate a seasonal climate with a topographically lowered floodplain that was frequently inundated by floodwaters and clastics from levee breaches (Nadon, 1994). Furthermore, the overall thickness of the soil horizons around the spillway and throughout the upper St. Mary River Formation suggests that much of the depositional history of the formation is preserved in outcrop (Nadon, 1994).

Paleoclimate

Globally, the Late Cretaceous period (99-65 Ma) appears to be significantly warmer (Wolfe and Upchurch, 1987; Spicer and Chapman, 1990; Crame, 1992; Frakes et al., 1992; Huber and Watkins, 1992), more or less ice-free (Spicer and Parrish, 1990; DeConto et al., 2000) and shows higher levels of atmospheric O_2 and CO_2 compared to the present (Crowley and Zachos, 2000; Berner et al, 2000). Some estimates put the global mean annual surface temperature at 8-10°C warmer than present, resulting in ice-free polar regions and temperate polar forests (Spicer and Parrish, 1990; Crowley and Kim, 1995; DeConto et al., 1998), while tropical sea surface temperatures may have been as high as 28-32 °C (Pearson et al., 2001). Although O_2 levels slowly decreased throughout the Late Cretaceous, it is estimated that O_2 constituted 26 to 28% of the Late Cretaceous atmospheric gases, compared to 21% at present (Berner, 1999; Berner et al, 2000). The elevated O_2 levels during this period, in combination with a warm and humid climate, higher temperatures and elevated atmospheric CO_2 from pole to pole, probably increased plant productivity globally. Consequently, a worldwide accumulation of biomass during the Late Cretaceous is recorded in the fossil record. This productivity is seen today as vast coal reserves in the middle to high latitude regions of the Northern Hemisphere and to a lesser extent the Southern Hemisphere (Spicer and Parrish, 1990). For example, the high latitude, mixed forest lowland plant communities of the Late Cretaceous on the North Slope of Alaska contain one-third of the US coal reserves. The paleogeographic position of this region in the Maastrichtian was believed to be near

85°N, further documenting a warmer than present polar climate (Smith et al, 1981; Spicer and Parrish, 1990).

Atmospheric CO_2 was also 1.5 to 5 times higher during the Late Cretaceous relative to today (Andrews et al., 1995; Berner, 1997; Berner and Kothavala, 2001; Beerling et al, 2002). The elevated level of CO_2 both increased the carbon available for plant photosynthesis and contributed to higher paleotemperatures globally (Spicer and Parrish, 1990). Again, the abundant coal reserves found at middle to high paleolatitudes during this epoch are evidence, at least in part, to a 'greenhouse' climate resulting from increased levels of atmospheric CO_2 that supported a highly productive plant community over a long period of time from pole to pole (McCabe, 1984; Spicer and Parrish, 1990; Berner and Kothavala, 2001). Royer et al. (2002) suggest that overall temperatures may have been warmer than predicted. They indicate that coldest mean month temperatures should be further increased in models by 1.5 to 3°C to account for higher CO_2 levels. Apparently, higher CO_2 levels lower the freezing point of leaves by this amount. Thus, temperature ranges may have fluctuated far less than predicted on a global scale or may have been seasonally warmer than predicted, particularly in continental interiors. This allowed frost-sensitive species, such as palms, to inhabit paleolatitudes as high as 70°N (Horrell, 1991). It should be noted that although the global climate was warmer than today, the longer term temperature trend throughout the Late Cretaceous indicates a general cooling of both hemispheres (Spicer and Parrish, 1990; Behrensmeyer et al., 1992). During the Campanian and Maastrichtian, northern high paleolatitude plant communities (75°-85°N) reflect a significant drop in mean annual temperature (Spicer and Parrish, 1990). This cooling is accompanied by increasing periods of aridity documented in pollen assemblages, growth rings, and facies changes that occur in the latest Campanian and late Maastrichtian of western Canada and Alaska (Sweet, 1989; Spicer and Parrish, 1990). So, overall the global climate cooled and dried in the Late Cretaceous.

Even as temperatures cooled (Spicer and Parrish, 1990) sea levels fell globally (on average) throughout the Campanian and Maastrichtian (Ziegler and Rowley, 1998), vegetation thrived in warm coastal plain environments worldwide (Spicer and Parrish, 1990; Blakey, 2001; Scotese, 2001). In North America, vast swamps covered lowland areas on the eastern side of the Cordillera (Srivastava, 1970; McCabe, 1984). This is evidenced by the vertical range and lateral extent of coal deposits for this period in Alberta and Saskatchewan through to Colorado and New Mexico (Roberts et al., 2003). In fact, the Horseshoe Canyon and Scollard Formations hold the most abundant coal reserves on the Alberta Plains (McCabe et al., 1986; Fig. 2.4). It also appears that the higher-grade coals are associated, at least in Alberta, with the many marine tongue incursions of the seaway (McCabe et al., 1986). This indicates that the aerially extensive peat swamps that paralleled the shoreline and penetrated 30-50 km inland were due, in part, to the presence of the inland seaway (McCabe et al., 1986). Given that the position of the northwestern shore of the Bearpaw Sea in the late Campanian to early Maastrichtian lay in central-southeastern Alberta (Lerand, 1983), it is probable that the sea contributed to moister and warmer regional paleoclimates due to the moderating effect that large bodies of water have upon surrounding air and land masses (Valdes et al., 1996; Ziegler and Rowley, 1998). Earlier studies of sedimentary environments around central and southern Alberta, lead Rahmani (1984) to conclude that the Late Cretaceous climate for this region was a humid coastal environment similar to the present day Gulf of Mexico, a conclusion that has been corroborated by later workers (i.e., Hamblin, 1998c; Eberth, 2002). This climatic setting is often used as a generalized model to represent the entire province thereby downplaying the unique depositional setting of the St. Mary River Formation. Barring these regional climatic differences, the Late Cretaceous climate in Alberta was different from modern coastal settings. Among other factors, the extreme surface to depth ratio (25,000:1) of this shallow inland sea (Ziegler and Rowley 1998), lead Slingerland et al. (1996) to conclude that the sea was strongly influenced by regional climate. Ziegler and Rowley (1998) indicated that local temperature, wind direction and freshwater input created annual and regional fluctuations in sea temperature and salinity that generated a constantly varying sea environment, affecting both marine and coastal flora and fauna. It seems reasonable to conclude that elevated paleotemperatures, increased levels of O_2 and CO_2, and close proximity to a large inland seaway (the Bearpaw Sea) that fluctuated seasonally in salinity levels and water temperature (not to mention the frequent transgressive and regressive phases), created a very different environment from the modern Gulf of Mexico. It is in this paleoclimate that the Late Campanian and Maastrichtian flora and fauna of Alberta evolved.

The Horseshoe Canyon and the St. Mary River formations in central and southwestern Alberta represent two climatically distinct but interfingering regions (Fig. 2.2). The Horseshoe Canyon Formation to the north is considered to be a humid, subtropical lowland with swamps and rainforest vegetation below the Drumheller Marine Tongue and a moist, temperate forest above (Srivastava, 1970). In contrast, the upper St.

Mary River Formation to the south is characterized as a semi-arid, seasonal wetland with numerous marshes and lakes (Nadon, 1993). The area where the two formations interfinger (surficially around the town of Champion, Alberta), shifted spatially through time; hence, the area that each formation covers expanded and contracted with time (Hamblin, 1998c; Canadian Society of Petroleum Geologists, 2000; Eberth, 2002). This dynamic change in surface area was probably due to allocyclic controls, primarily regional tectonic activity and sea-level change (Hamblin, 1998c; Eberth, 2002). However, a relatively stable, long-term zonation in regional climate was noted by Jerzykiewicz and Sweet (1988), suggesting that a wet north and dry south climatic zonation in Alberta existed from the Early Cretaceous to the present. This could indicate that factors such as the topography of the Cordilleran ranges of northwestern North America and prevailing wind directions (among other possibilities, including global air circulation patterns and solar input) might have maintained this relatively constant wet/dry climate zonation for over 100 Ma (Art Sweet pers. commun., 2003). Both formations also indicate a gradual increase in aridity from the late Campanian to the late Maastrichtian (Srivastava, 1970; Nadon, 1998; Eberth, 2002). This increase in aridity, in turn, was correlated with the regression of the Bearpaw Sea, also suggesting that the regional climate was strongly influenced by changes in sea-level (Spicer and Parrish, 1990). Thus, a greater understanding of the allocyclic controls affecting the region should increase our understanding as to why a north to south climatic zonation existed for so long. Moreover, recognition of this wet/dry zonation provides an opportunity to study how plant communities adapted to each environment and the patterns of migration and evolutionary changes that resulted as the climate changed.

To date, Nadon (1991, 1993, 1994) has attempted to reconstruct the upper St. Mary River Formation. Using modern analogs (generally considered to be savannas), Nadon (1994) suggests that an annual peak in the hydrograph combined with low gradient slopes are characteristic of anastomosed system deposits. Nadon (1994) also noted that it is common in the modern systems for peak flow to occur in the spring or summer from meltwater or from seasonal precipitation in nearby upland areas. This indicates that constraints on the paleoclimate and paleoslope are probable. Unfortunately, there is not enough information currently available on the megaflora from the St. Mary River Spillway fossil locality or other fossil localities from the formation (Bell, 1965; Riley and Stockey, 1999) to corroborate Nadon's (1994) hypothesis on mean annual precipitation (Wilf et al., 1998) or the possibility of seasonal peaks in the hydrograph.

Understanding the effects of climate change on the paleoflora also requires reconstructing depositional environments and describing communities using abundance and diversity data. Since the depositional environments, fauna, and to a much lesser extent the flora of the Horseshoe Canyon Formation are relatively well documented compared to the St. Mary River Formation (Serbet, 1997; Hamblin, 1998c), future studies on the St. Mary River Formation are necessary. The St. Mary River Formation is an important link in understanding the southern Alberta fossil plant communities and the effect that regional climate had upon the distribution and evolution of this biota. For example, as the regional climate dried into the late Maastrichtian (Eberth, 2002), did plant communities inhabiting the semi-arid St. Mary River Formation migrate north? To date, there is not enough information on the flora to suggest migration or even overlap of taxon ranges. Thus, future excavations are needed for a more thorough account of the megaflora in order to understand the St. Mary River Formation plant communities and the effects that climate change had on the region.

Work on the abundant and well-preserved fossil taxa from the St. Mary River Spillway locality is underway (Riley and Stockey, 1999; Table 2.1). A fossil assemblage of at least 32 species of vascular plants, many of them aquatic, has been documented from various microenvironments at the locality (Rothwell and Stockey, 1994; Stockey and Rothwell, 1997; Riley and Stockey, 1999, 2000; Table 2.1). Understanding of the composition and habitats of these rarely described seasonal wetlands from the upper St. Mary River Formation has improved, but is still in the early stages of study (Riley and Stockey, 1999; Table 2.1).

Studies of extant plant communities indicate that leaf margin characters from woody angiosperms are good indicators of mean annual temperature (MAT). (Wolfe, 1979, 1993; Wilf, 1997). Wilf (1997) has shown that one character in particular, toothed versus entire margins, provides excellent estimates of MAT, provided moisture is not limiting and/or temperatures extremely cold. Consequently, paleobotanists have used these characters to estimate paleotempertures for many years as this provides a possible tool to reconstruct past climates (Bailey and Sinnott, 1916; Wolfe, 1979; Wilf, 1997). A univariate linear regression technique known as Leaf Margin Analysis (LMA) (Wing and Greenwood, 1993) was performed to estimate the MAT. The MAT of site 2 is about 13°C with a standard deviation of ±4°C (appendix D; Wilf, 1994). This would categorize the fossil locality as a mesothermal climate (13-20°C) or possibly a microthermal climate (<13°C) (Wolfe, 1979). Without a mean annual range in temperature, it is difficult to categorize the community type using Wolfe's (1979) nomogram for thermal domains occupied by extant humid forests. Using the MAT of 13°C, the paleocommunity could range from a mixed broad-leaf deciduous forest to a microphyllous broad-leaved evergreen forest. However, the use of nearest living relative analogs must be used with caution as stasis in physiognomic adaptations and environmental range is assumed in the LMA (Spicer and Parrish, 1990). In addition, the small number of 'woody' angiosperm specimens recovered and the low taxon count (eight toothed and five entire margined taxa) could bias the temperature predictions since they are a poor sample of the surrounding communities constituting a non-random sample (Wilf, 1997). Furthermore, the woody angiosperm leaves were primarily found in splay sandstones and could be considered parautochthonous to allochthonous deposits washed in from riparian habits upstream (Gastaldo et al., 1996; Gastaldo and Ferguson, 1998). This potentially biased sampling could underestimate the MAT by as much as 5°C (Wilf, 1997; Burnham et al. 2001). Wilf (personal commun., 2003) indicated that higher taxon counts and increased sample sizes from various depositional settings helps to reduce error in MAT estimates. Therefore, a more extensive sampling of the locality should be undertaken.

In addition to previously mentioned depositional evidence for a seasonally wet climate, several fossil taxa recovered from the St. Mary River Spillway locality could indicate seasonal peaks in water flow. The modern representatives of *Equisetum*, *Metasequoia* Miki, *Ginkgo* L., *Platanus* L., and *Typha* L. are considered both drought and flood tolerant (Table 2.1). Deciduous taxa such as *Ginkgo* L., *Platanus* L., *Zizyphoides* Seward and Conway, and taxodiaceous spp. could also indicate a physical response to seasonally dry conditions, although other factors such as cool temperatures, seasonal light fluctuations (due to latitude), nutrient flux, and infection or damage could also account for deciduousness. Again, the extrapolation of present habitat and physiological adaptations in living plants to fossil taxa (especially as old as the Late Cretaceous) should be interpreted with caution when used as an independent data set (Spicer and Parrish, 1990). Nonetheless, when combined with data that indicates a semi-arid, seasonal wet setting (Nadon, 1994), water limiting conditions could account for deciduousness. Further studies of growth rings of the *in situ* wood found throughout the formation (Nadon, 1994) might also improve our understanding of the water regime.

Tracing the facies changes stratigraphically from the lowermost to uppermost bedding sequences at the St. Mary River Spillway indicates possible climatic zones or microenvironments. The lowermost beds, exposed downstream from the spillway (Fig. 2.7a, to the left of the photo), show thin caliche horizons and no visible coal seams, possibly indicating a semi-arid or seasonally dry depositional setting (Jerzykiewicz and Sweet, 1988). (Caliche glaebules are terrestrial calcium carbonate nodules or concretions commonly found in soil profiles associated with semi-arid to arid environments.) The Lower Mudstone unit underlaying the Spillway (Fig. 2.7a), site 1(Fig. 2.7a), site 2 (Fig. 2.6a), and the Massive Sandstone unit (Fig. 2.7a) reflect wetter conditions with rare coal seams (Fig. 2.8a) appearing near the base of the Massive Sandstone unit, abundant plant remains and no visible caliche zones. The palynological samples taken for the upper part of this sequence also indicate a swampy, backwater fluvial to lacustrine setting (Sweet, 1999, Appendix A, Sample P4454-1 to P4454-5). Caliche horizons again appear above the Massive Sandstone unit (Fig. 2.7a) indicating a drier interval of time which is noted in the palynological samples (Sweet, 1999, Appendix A, Sample P4454-6). The miospore samples (Sweet. 1999, Appendix A, sample P4454-7) recovered from the uppermost section, and the return of thick siltstone and mudstone floodplain deposits (Fig. 2.8a), again suggest a wetter climate. The interpretation of successive wet and dry intervals might represent local microenvironments or possible changes in regional or global paleoclimate. Further paleobotanical and sedimentological studies from the St. Mary River Spillway locality and other exposures of the St. Mary River Formation might help to indicate whether these proposed climatic changes are local or wider ranging. In the future, by tracing the floral change in vertical succession through the St. Mary River and Horseshoe Canyon Formations, a more comprehensive picture of local and regional paleoclimate and paleoenvironments for this age in Alberta should be possible.

The content of this chapter includes a review of previously published literature and the presentation of new material and ideas by the author. The review was undertaken to present the reader with background information on currently held ideas about the paleoenvironments and paleoclimate of the Cretaceous period and the Campanian and Maastrichtian ages in particular. My contributions include the analysis and interpretation of the depositional environment at the St. Mary River Spillway locality (including the paleocurrent direction), and the paleotemperature estimate using Leaf Margin Analysis to interpolate Mean Annual Temperature. The palynological studies used to estimate the age of the locality were undertaken, primarily, with the help of Art Sweet (see Appendix A).

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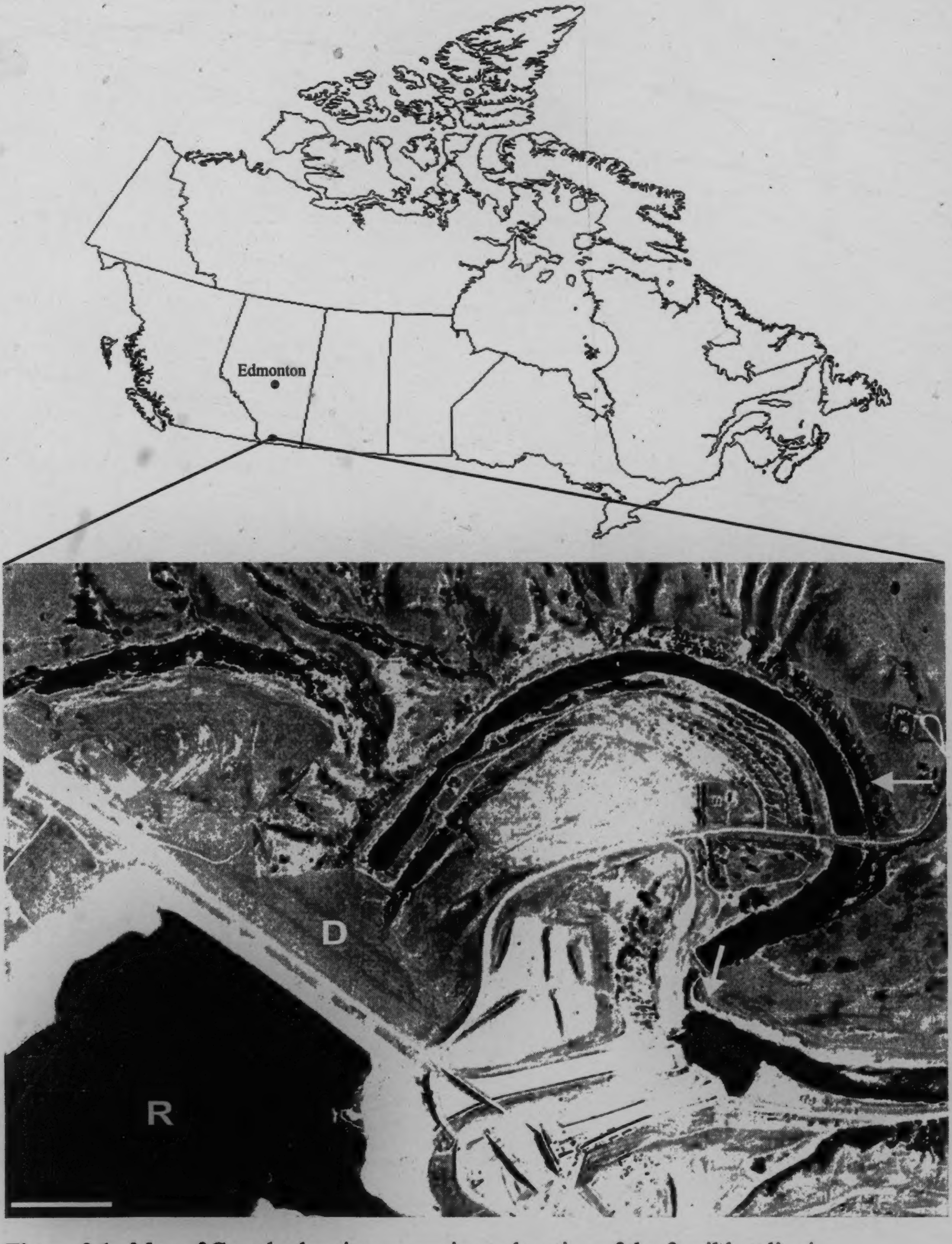


Figure 2.1. Map of Canada showing approximate location of the fossil locality in southwestern Alberta. Air photo of the St. Mary Reservoir (R) and Dam (D). Upper arrow shows location of site 2 and lower arrow of site 1. Air photo from the Alberta Government (2000). Scale bar = 300 m.

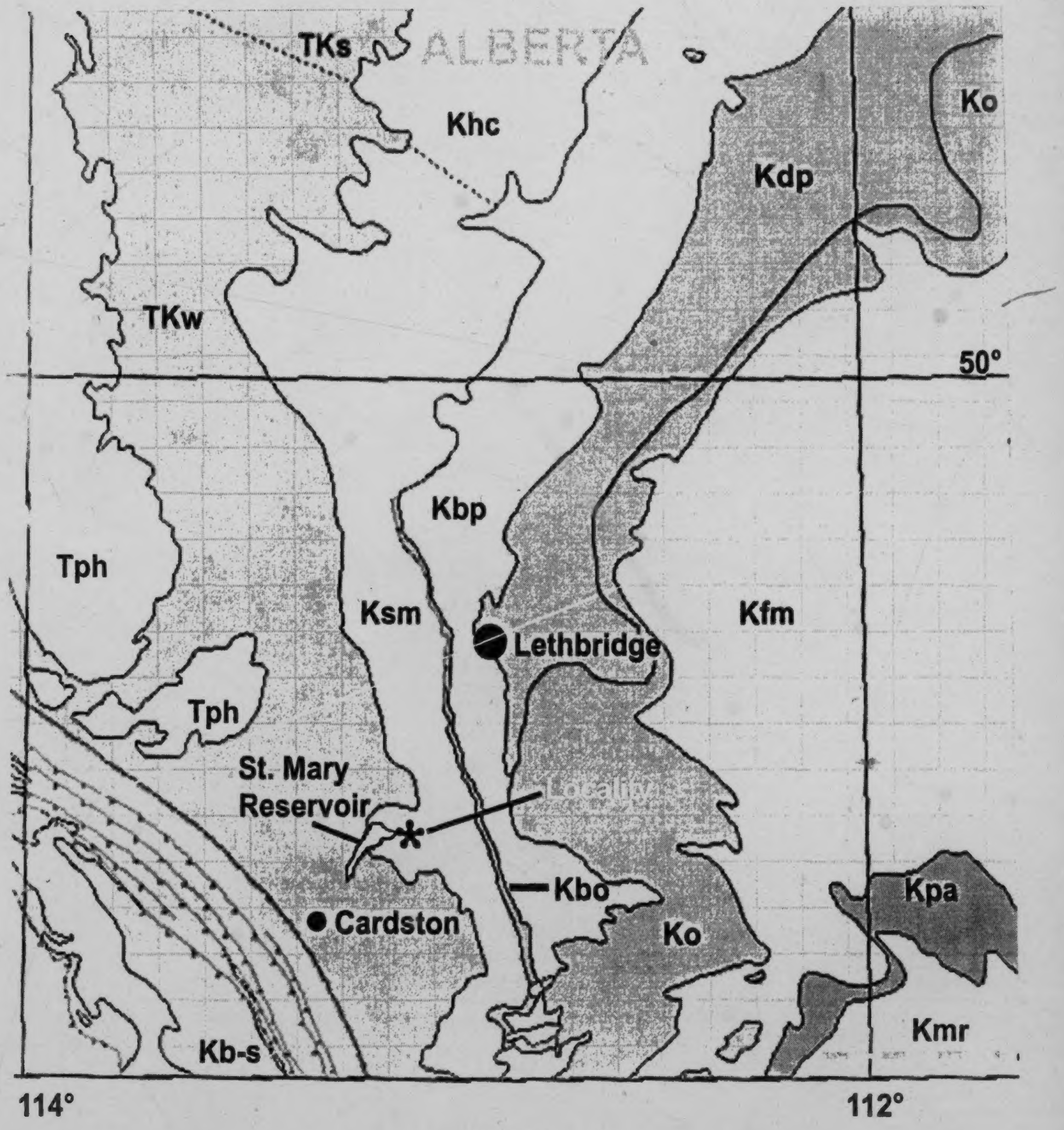

TKs
ALBERTA
Khc
Ko
Kdp
TKw
50°
Kbp
Tph
Ksm
Kfm
Lethbridge
Tph
St. Mary
Reservoir
Locality
Kbo
Cardston
Ko
Kpa
Kmr
Kb-s
114°
112°

Figure 2.2. Surficial geologic map of southwestern Alberta showing boundaries of uppermost Cretaceous and lower Tertiary formations, after Canadian Society of Petroleum Geologists (2000). For a photo of the locality see Figure 2.1. Formation symbols are defined in the List of Symbols and Abbreviations section. White line indicates approximate location of regional cross section in Figure 2.3. Scale bar = 30 km.

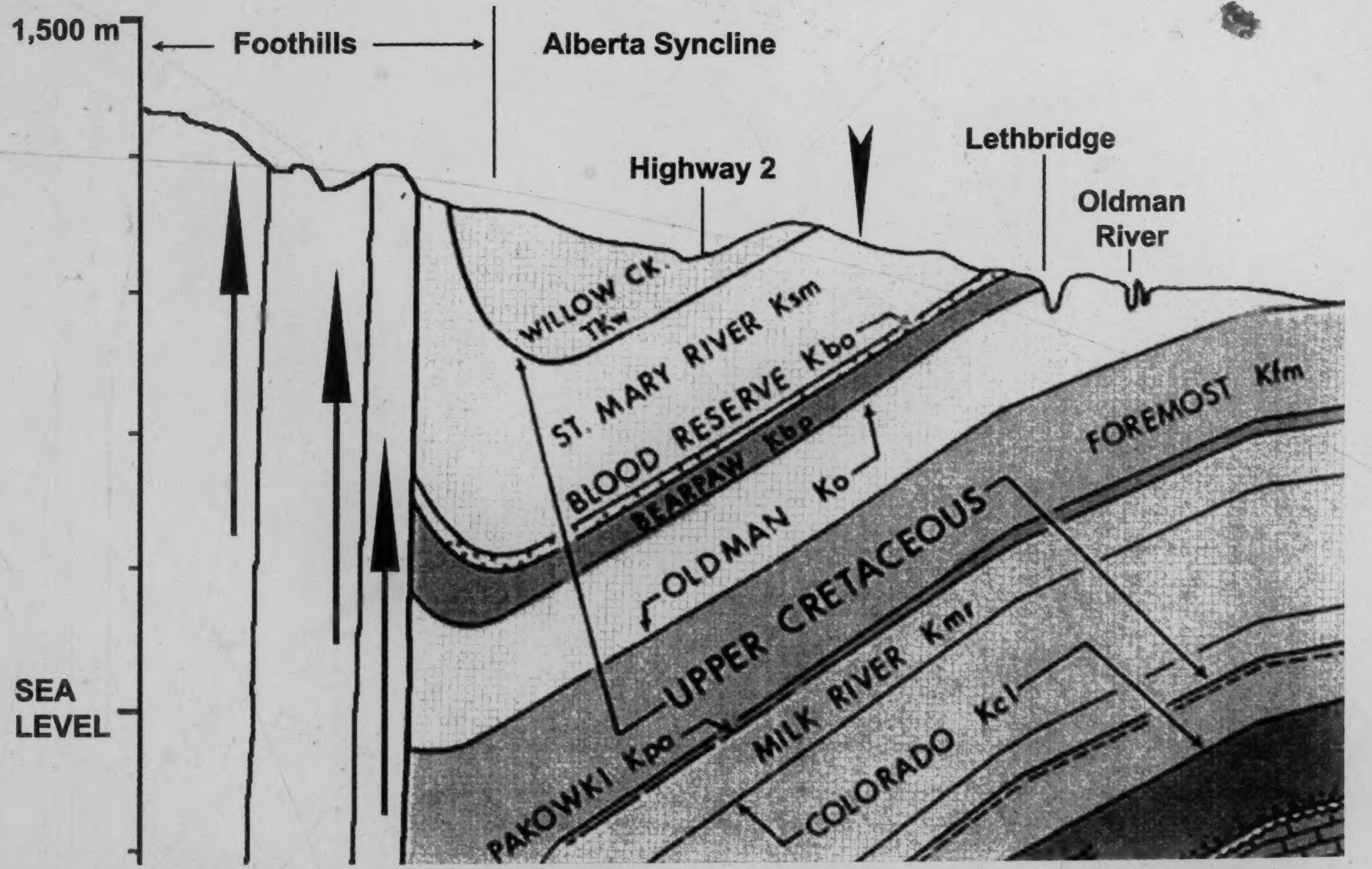

1,500 m
Foothills
Alberta Syncline
SEA LEVEL
Highway 2
Lethbridge
Oldman River
WILLOW CK. TKw
ST. MARY RIVER Ksm
BLOOD RESERVE Kbo
BEARPAW Kbp
OLDMAN Ko
FOREMOST Kfm
UPPER CRETACEOUS
PAKOWKI Kpo
MILK RIVER Kmr
COLORADO Kcl

Figure 2.3. Regional Cross Section through southwestern Alberta (see Fig. 2.2 for approximate location of transect). Modified from the Canadian Society of Petroleum Geologists (1981). The St. Mary Reservoir fossil locality is approximately 20 km south of the arrow head.

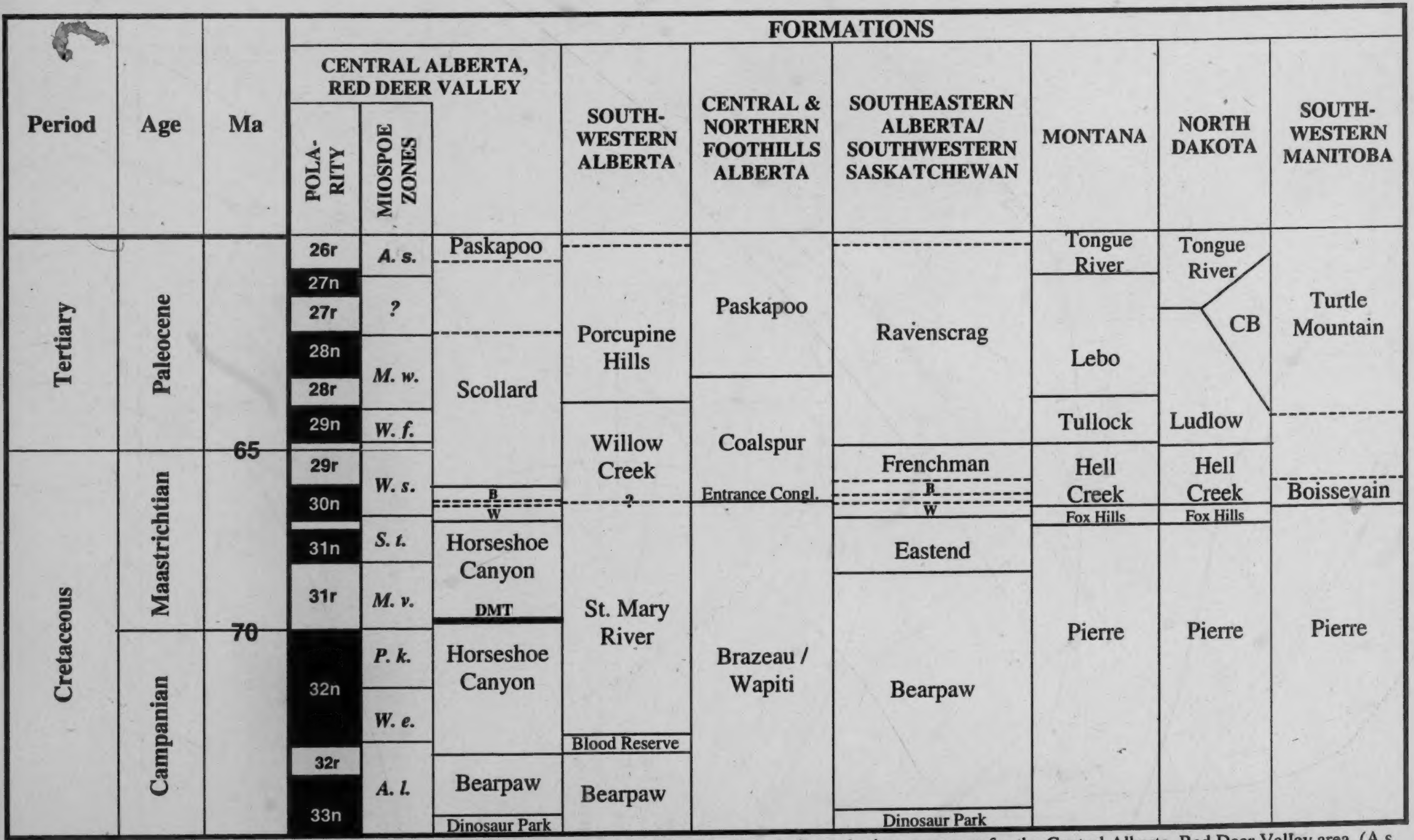
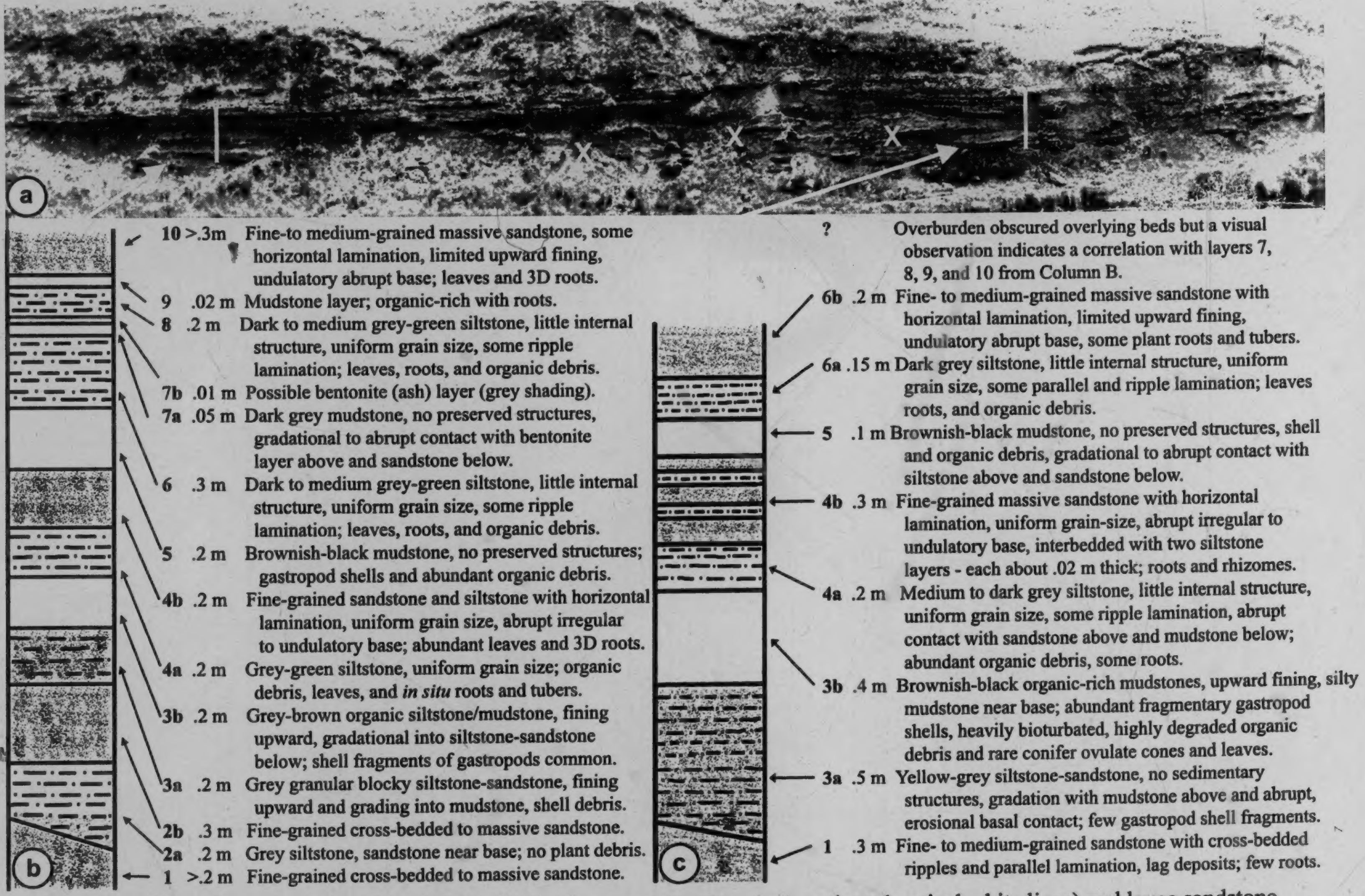

FORMATIONS
Period
Age
Ma
CENTRAL ALBERTA, RED DEER VALLEY
POLA-RITY
MIOSPOE ZONES
SOUTH-WESTERN ALBERTA
CENTRAL & NORTHERN FOOTHILLS ALBERTA
SOUTHEASTERN ALBERTA/ SOUTHWESTERN SASKATCHEWAN
MONTANA
NORTH DAKOTA
SOUTH-WESTERN MANITOBA
Tertiary
Cretaceous
Paleocene
Maastrichtian
Campanian
65
70
26r
27n
27r
28n
28r
29n
29r
30n
31n
31r
32n
32r
33n
A. s.
?
M. w.
W. f.
W. s.
S. t.
M. v.
P. k.
W. e.
A. l.
Paskapoo
Scollard
B
W
Horseshoe Canyon
DMT
Horseshoe Canyon
Bearpaw
Dinosaur Park
Porcupine Hills
Willow Creek
?
St. Mary River
Blood Reserve
Bearpaw
Paskapoo
Coalspur
Entrance Congl.
Brazeau / Wapiti
Ravenscrag
Frenchman
B
W
Eastend
Bearpaw
Dinosaur Park
Tongue River
Lebo
Tullock
Hell Creek
Fox Hills
Pierre
Tongue River
CB
Ludlow
Hell Creek
Fox Hills
Pierre
Turtle Mountain
Boissevain
Pierre

Figure 2.4. Correlation of uppermost Cretaceous and earliest Tertiary strata in Alberta with polarity and miospore zones for the Central Alberta, Red Deer Valley area. (A.s. = *Aquilapollenites spinulosus* Funkhouser; M.w. = *Momipites wyomingensis* Nichols and Otte; W.f. = *Wodehousia fimbriata* Stanley; W.s. = *Wodehousia spinata* Stanley; S.t. = *Scollardia trapaformis* Srivastava; M.v. = *Mancicorpus vancampoi* Srivastava; P.k. = *Pulcheripollenites krempii* Srivastava; W.e.= *Wodehousia edmonticola* Wiggins; A.l. = *Aquilapollenites leucocephalus* Srivastava; W = Whitemud Formation; B = Battle Formation; DMT = Drumheller Marine Tongue; CB = Cannonball Formation; - - - = missing time.) After Demchuk (1990), McIver and Basinger (1993), Braman and Sweet (1999), Catuneanu and Sweet (1999), Lerbekmo (1999), Lerbekmo et al. (1992), Lerbekmo and Braman (2002), Sweet (2001).



Bed	Thickness	Description
10	>.3m	Fine-to medium-grained massive sandstone, some horizontal lamination, limited upward fining, undulatory abrupt base; leaves and 3D roots.
9	.02 m	Mudstone layer; organic-rich with roots.
8	.2 m	Dark to medium grey-green siltstone, little internal structure, uniform grain size, some ripple lamination; leaves, roots, and organic debris.
7b	.01 m	Possible bentonite (ash) layer (grey shading).
7a	.05 m	Dark grey mudstone, no preserved structures, gradational to abrupt contact with bentonite layer above and sandstone below.
6	.3 m	Dark to medium grey-green siltstone, little internal structure, uniform grain size, some ripple lamination; leaves, roots, and organic debris.
5	.2 m	Brownish-black mudstone, no preserved structures; gastropod shells and abundant organic debris.
4b	.2 m	Fine-grained sandstone and siltstone with horizontal lamination, uniform grain size, abrupt irregular to undulatory base; abundant leaves and 3D roots.
4a	.2 m	Grey-green siltstone, uniform grain size; organic debris, leaves, and *in situ* roots and tubers.
3b	.2 m	Grey-brown organic siltstone/mudstone, fining upward, gradational into siltstone-sandstone below; shell fragments of gastropods common.
3a	.2 m	Grey granular blocky siltstone-sandstone, fining upward and grading into mudstone, shell debris.
2b	.3 m	Fine-grained cross-bedded to massive sandstone.
2a	.2 m	Grey siltstone, sandstone near base; no plant debris.
1	>.2 m	Fine-grained cross-bedded to massive sandstone.

Bed	Thickness	Description
?		Overburden obscured overlying beds but a visual observation indicates a correlation with layers 7, 8, 9, and 10 from Column B.
6b	.2 m	Fine- to medium-grained massive sandstone with horizontal lamination, limited upward fining, undulatory abrupt base, some plant roots and tubers.
6a	.15 m	Dark grey siltstone, little internal structure, uniform grain size, some parallel and ripple lamination; leaves roots, and organic debris.
5	.1 m	Brownish-black mudstone, no preserved structures, shell and organic debris, gradational to abrupt contact with siltstone above and sandstone below.
4b	.3 m	Fine-grained massive sandstone with horizontal lamination, uniform grain-size, abrupt irregular to undulatory base, interbedded with two siltstone layers - each about .02 m thick; roots and rhizomes.
4a	.2 m	Medium to dark grey siltstone, little internal structure, uniform grain size, some ripple lamination, abrupt contact with sandstone above and mudstone below; abundant organic debris, some roots.
3b	.4 m	Brownish-black organic-rich mudstones, upward fining, silty mudstone near base; abundant fragmentary gastropod shells, heavily bioturbated, highly degraded organic debris and rare conifer ovulate cones and leaves.
3a	.5 m	Yellow-grey siltstone-sandstone, no sedimentary structures, gradation with mudstone above and abrupt, erosional basal contact; few gastropod shell fragments.
1	.3 m	Fine- to medium-grained sandstone with cross-bedded ripples and parallel lamination, lag deposits; few roots.

Figure 2.5. a), Photomosaic of site 2 showing position of two measured vertical sections (vertical white lines) and levee sandstone region (X's). Outcrop is 105 m long. **b & c)**, Vertical sections with thickness measurements and descriptions for each noted bed. Sections are roughly to scale.

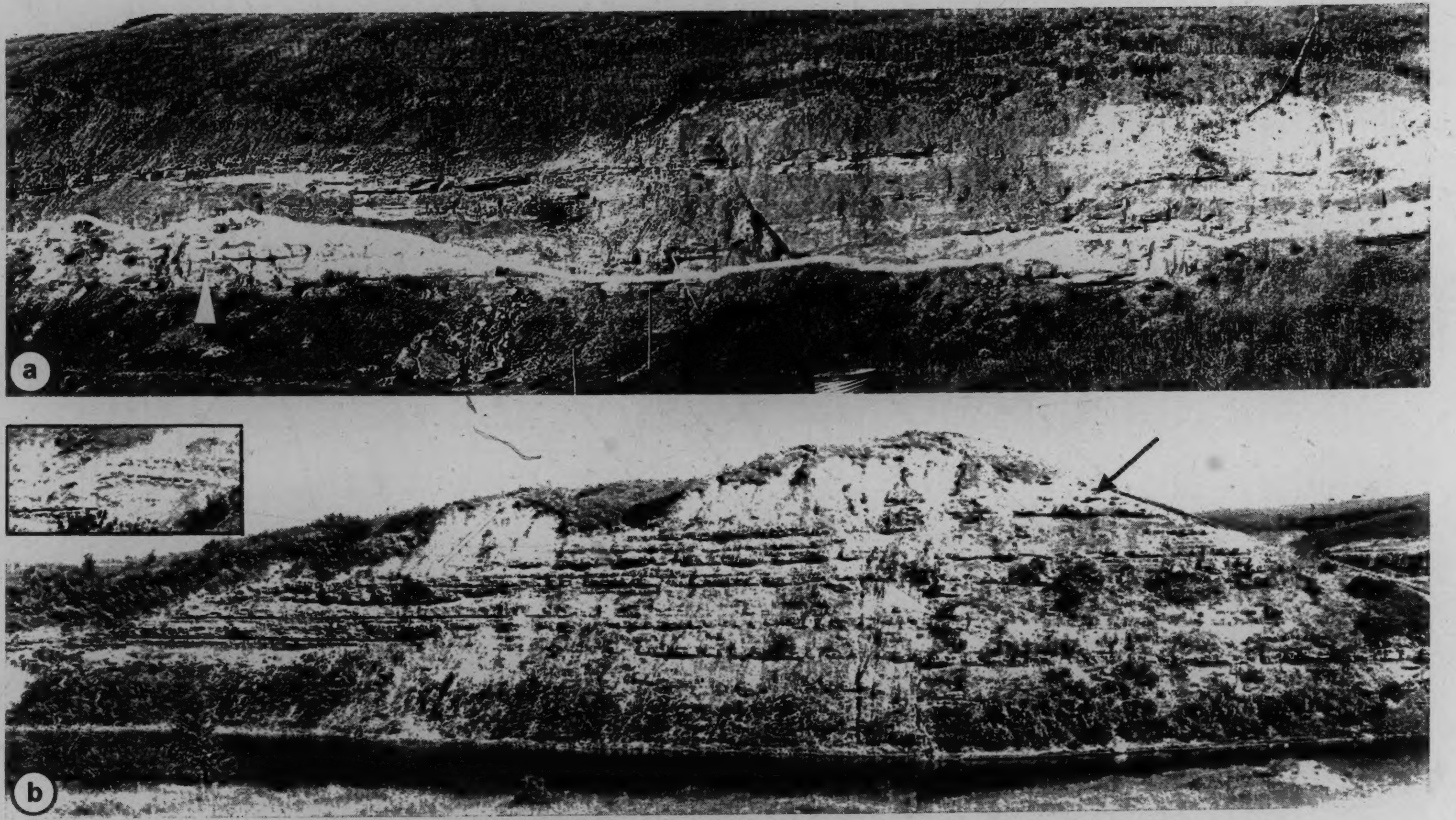


Figure 2.6. **a**), Photomosiac showing part of site 2 at St. Mary River Spillway. White line traces disconformity (erosional surface) separating underlying levee and channel sandstones from overlying lacustrine, marsh, and crevasse splay deposits. Arrowhead indicates levee deposits. Outcrop is 40 m long. **b**), Photomosaic of site 1.5 showing facies profile typical of St. Mary River Formation. All four facies associations (Nadon, 1994) are represented here: channel and levee (arrows), splay-channel (arrowhead), crevasse-splay sheets (thin, horizonal, protruding beds), and floodplain environments (darker, thin, horizontal, recessed beds between crevasse-splay sheets). Black arrow corresponds to Massive Channel Sandstone unit. Outcrop is 180 m long. Inset shows 4 m high fold in outcrop to left of photo (white line).

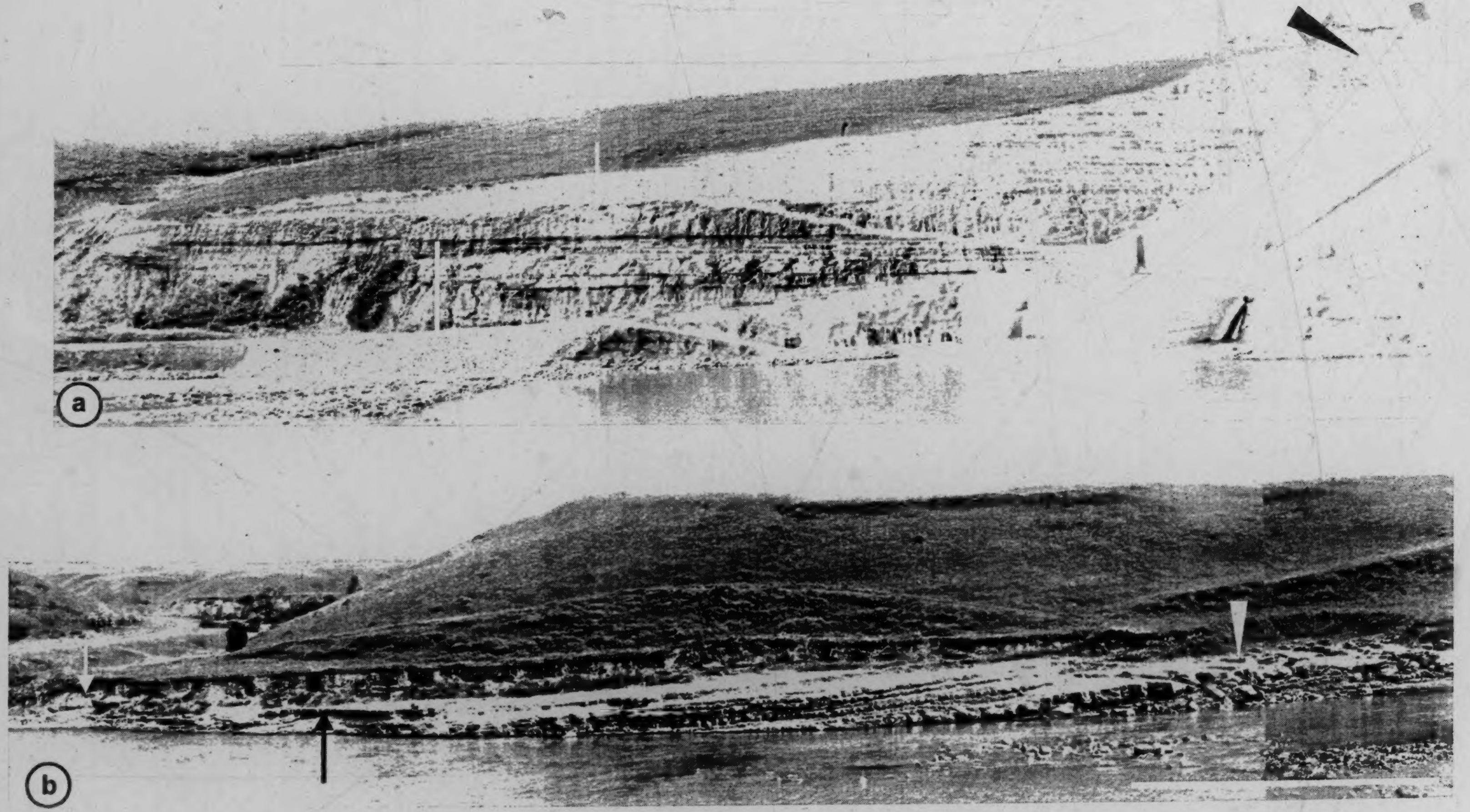


Figure 2.7. **a**), Photomosaic of site A showing new spillway and recent exposure from spillway construction. Lower Siltstone and Sandstone unit (vertical line). Massive Channel Sandstone unit (arrow) showing channel margin (wavy line). Upper Mudstone unit (arrowhead). Scale bar = 30 m. **b**), Photomosaic of site 1 (white arrow). Fluvial sandstones (arrowhead) showing large river channel underlying alternating pale yellow fine-grained sandstone (black arrow) and ripple laminated light grey fine-grained sandstone layers. Pale yellow sandstones layers are heavily burrowed with *Ophiomorpha*-like burrows. Scale bar = 30 m.

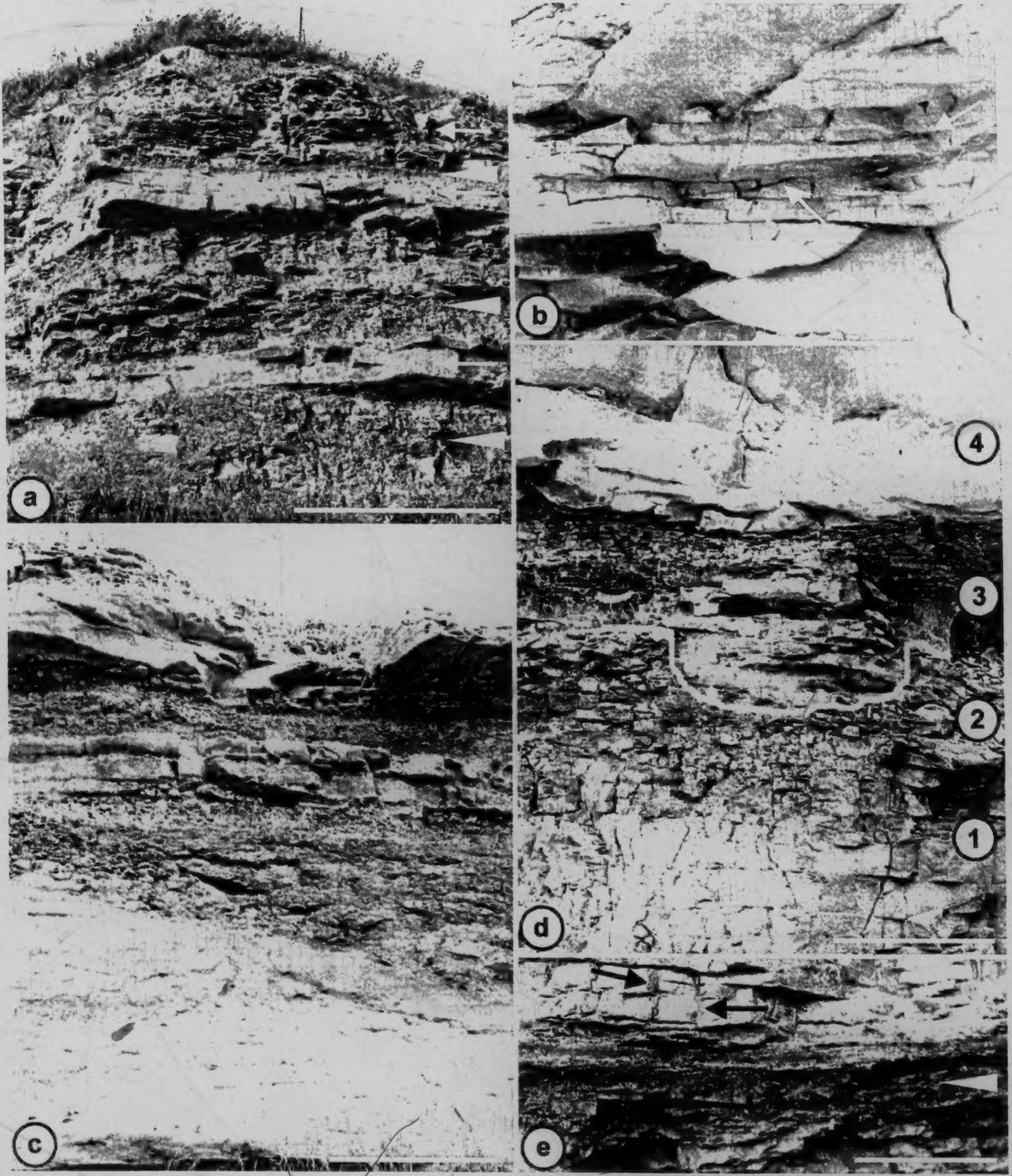


Figure 2.8. **a**), Stratigraphic sequence showing crevasse-splay sandstones (arrows) alternating with floodplain siltstones and mudstones (arrowhead) near site 6. Bar = 2 m. **b**), Sandstone crevasse-splay sheets showing horizonal and vertical roots and rhizomes (arrows) from site 2 (Canadian $1 coin for scale). **c**), Close-up of site 2 at 31 m mark (see Figure 2.5 for details). Bar = 1 m. **d**), Depositional sequence from site 2 showing paleosol horizon (1 = sandstone-siltstone; 2 = mudstone; 3 = siltstone; 4 = sandstone). Note possible dinosaur track (line). Bar = 30 cm. **e**), Rare coal layer (arrowhead) near site 4. Notice straight, thin, vertically oriented, and evenly distributed roots (arrows). Bar = 10 cm

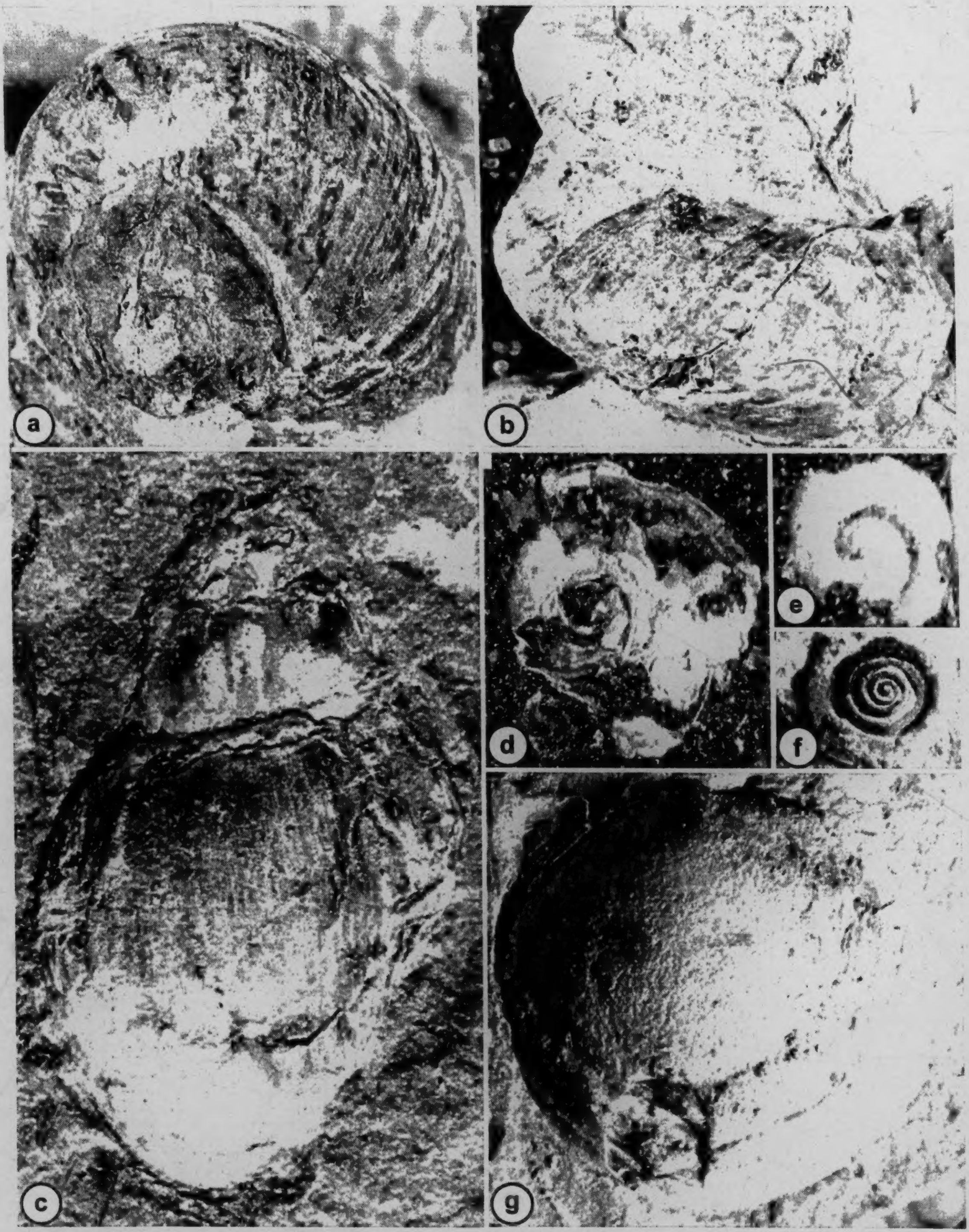


Figure 2.9. **a**), *Viviparus* sp. from site 2. S57,616. x2.5. **b**), *Viviparus* sp. from site 2. S58,249. x 2.5. **c**), *Lioplacodes*-like sp. from site 2. S58,250A. x 12. **d & e**), *Planorbis*-like sp. from site 2. S58,245. x 40 & x 75, respectively. **f**), *Biomphalaria*-like sp. from site 1. Outcrop photo. x 2. **g**), *Sphaeriidae*-like sp. from site 0. S58251. x 14.

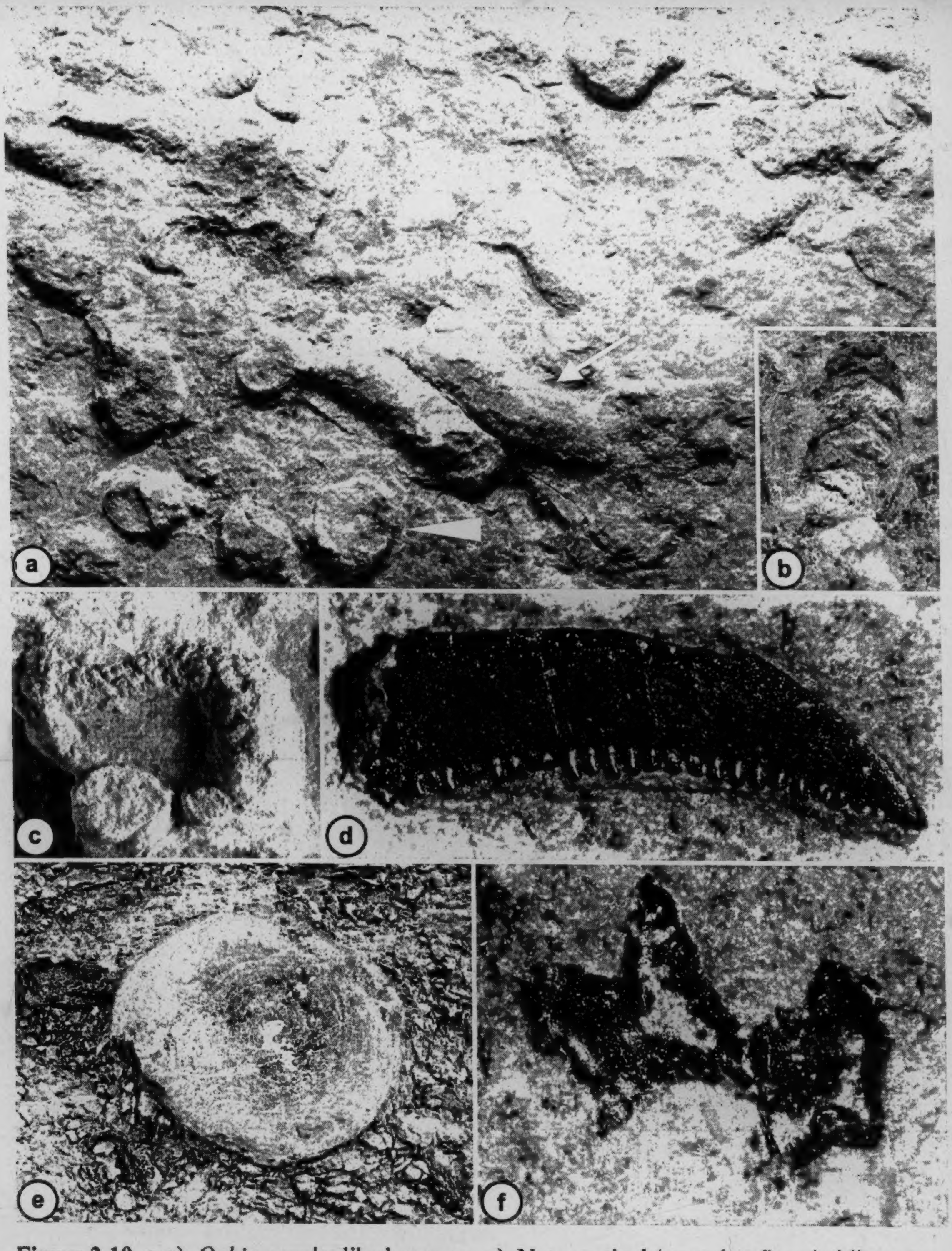


Figure 2.10. a-c), *Ophiomorpha*-like burrows. **a**), Note vertical (arrowhead) and oblique to horizontal (arrow) traces in sandstone. S58370A & B. x 0.5. **b**), Burrow longitudinal section showing backfilling. S58370A. x 1.6. **c**), Burrow showing knob-like pelletal lining (arrow). S58370A. x 1. **d**), Serrated theropod tooth. UALVP 45,699. x 13. **e**), Ceratopsid cervical vertebra *in situ* near site D. x 0.6. **f**), Probable marsupial lower molar. UALVP 45,698. x 15.

Table 2.1: Systematics of Flora from the St. Mary River Spillway Fossil Locality.

Kingdom Plantae
Division Tracheophyta

Class Lycopsida
Family Isoetaceae
Isoetites Münster sp.

Class Sphenopsida
Family Equisetaceae
Equisetum L. sp.

Class Filicopsida
Family Dryopteridaceae
Onoclea L. sp.
Family Hydropteridaceae
Hydropteris pinnata Rothwell et Stockey

Class Ginkgoopsida
Family Ginkgoaceae
Ginkgo L. sp.

Class Coniferopsida
Family Cupressaceae
Metasequoia Miki sp.
cf. *Taxodium* Richard sp.
2 unidentified taxa
Family Sciadopityaceae
Sciadopitys-like Siebold et Zuccarini sp.

Class Magnoliopsida

- Family Lauraceae
  - cf. *Araliaephyllum polevoi* (Kryshtofovich) Krassilov
- Family Platanaceae
  - cf. *Platanus* Linnaeus sp.
- Family Trochodendraceae
  - *Zizyphoides* Seward et Conway sp.
- Family *incertae sedis*
  - *Fortuna marsilioides* (Bell) McIver et Basinger
  - *Quereuxia angulata* (Newberry) Krysht. ex Baikovskaja
  - Large *Quereuxia*-like leaves, double-toothed, rosette forming, floating aquatic
  - Simple, petiolate leaves with reticulate venation and chloranthoid teeth ('Spoon')
  - 7 spp. unidentified leaves
  - Unidentified filiform-like aquatic
  - Unidentified fruits/seeds (6 taxa)

Class Liliopsida

- Family Limnocharitaceae
  - *Cardstonia tolmanii* Riley et Stockey
- Family Arecaceae
  - cf. *Sabal* Adanson sp.
- Family Typhaceae
  - cf. *Typha* Linnaeus sp.
- Family *incertae sedis*
  - 3 unidentified broad leaved forms (1 very large)
  - 1 unidentified strap-shaped form
  - Unidentified seeds/fruits

Chapter 3

Cardstonia tolmanii gen. et sp. nov. (Limnocharitaceae) from the Upper Cretaceous of Alberta, Canada**

Introduction

The well-preserved fossil plants from the Upper Cretaceous Cardston Flora of southern Alberta have yielded 32 taxa of predominantly aquatic plants (Riley and Stockey 1999). These plants are compression/impressions that in some cases are nearly complete due to rapid burial in fine-grained sediments. Geologic data suggest that they were buried *in situ* in shallow oxbow lakes or ponds during a period of rapid sedimentation (Riley and Stockey 2000). Only two plants have been described in detail and reconstructed as whole plants: *Hydropteris pinnata* Rothwell et Stockey (1994), a heterosporous fern, and *Quereuxia angulata* (Newberry) Krysht. ex Baikovskaja (Stockey and Rothwell 1997), a floating, rosette-forming dicot.

The Cardston site is remarkable in its preservation of large-leaved monocots. Broad leaves of these herbaceous plants are usually rare in the fossil record (Herendeen and Crane 1995). At least six types of monocot leaves (in addition to those of a sabaloid palm) are present in sediments of the St. Mary River Formation at Cardston. One of these monocot leaf types has been compared to leaves described as *Haemanthophyllum* Budantsev (1983) from the Late Paleocene - Early Eocene of western Kamchatka (Riley and Stockey 1998). This leaf-type was originally assigned to the Amaryllidaceae; however, further studies of leaf venation and comparisons to extant and fossil monocots

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** A version of this chapter has been submitted (2003) for publication: Riley, M.G. and R.A. Stockey, International Journal of Plant Sciences.

have led several workers to suggest relationships to Alismataceae, Potamogetonaceae and Aponogetonaceae (Heer 1868; Boulter and Kvaček 1989; Golovneva 1987, 1997). A number of leaves of differing morphology have been assigned to this genus (table 3.1) but their affinities remain in doubt (Golovneva 1997).

Several broad-leaved monocots generally conforming to *Haemanthophyllum* have been identified in the Cardston Flora (Riley and Stockey 1998). In this study we compare leaf morphology and detailed venation patterns of these Cretaceous leaves to fossils in the genus *Haemanthophyllum* and those of extant Aponogetonaceae, Alismataceae, Hydrocharitaceae, Stemonaceae, Potamogetonaceae, and Limnocharitaceae. We describe these remains as *Cardstonia tolmanii* Riley et Stockey gen. et sp. nov. and suggest that they have affinities to Limnocharitaceae.

Material and Methods

Fifty compression/impression specimens of leaves have been collected from three sites on the banks of the St. Mary River below the reservoir and spillway (fig. 3.1). Outcrops are part of the St. Mary River Formation, Upper Cretaceous, and are Late Campanian-Early Maastrichtian in age (Nadon 1988; Hamblin 1998; A. R. Sweet pers. commun., 2003).

Fossils come from alternating layers of siltstones and fine-grained sandstones that were deposited on the floodplains or the abandoned channels of an anastomosing river system. Most plants were preserved by rapid sedimentation in oxbow lakes or ponds (Nadon 1988). The best-preserved leaves are found in the siltstones. Specimens were prepared by degagement, photographed using a MicroLumina digital scanning camera (Leaf Systems, Inc.) and processed using Adobe Photoshop 6.0.

All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA) and carry specimen numbers S50,939; S50,940; S50,947; S50,955-S50,958; S50,988; S50,989: S52,263-S52,283; S52,292-S52,295; S55,129-S55,135; S55,137-S55,150; S55,154.

Leaves of extant monocots in the Alismataceae, Amaryllidaceae, Aponogetonaceae, Hydrocharitaceae, Limnocharitaceae, Potamogetonaceae, and Stemonaceae were examined during this study from fresh and herbarium specimens from the Munich Botanical Gardens, Herbarium of the Northern Territory, Darwin, Australia (DNA) and University of Alberta Vascular Plant Herbarium (ALTA) (table 3.2). Photographs were taken using both transmitted and reflected light (figs. 3.5a-3.5h).

Systematics

Order: Alismatales Lindley

Family: Limnocharitaceae Takhtajan

Genus: *Cardstonia* Riley et Stockey gen. nov.

Species: *C. tolmanii* Riley et Stockey sp. nov.

Generic diagnosis: Leaves simple, ovate to elliptic, margin entire; 5-12 cm long, 3.5-8.5 cm wide; l:w ratio: 1.4:1; apex convex to rounded; base cordate; petiole 3-4 mm wide, at least 2 cm long, petiolar attachment marginal. Venation campylodromous, 23-27 primary veins originating at or near base, running in strongly recurved arches that converge apically, merging at or near apex, three prominent primary veins form midrib area, prominent fimbrial vein present. Secondary veins diverging at low angles (45°) near midrib and higher angles near margin (90°); alternating major and minor secondary veins occasionally dichotomous. Tertiary veins few, irregular, thin; connecting adjacent secondaries; rarely forming irregular areolae.

Holotype. UAPC-ALTA S55138 (fig. 3.2a):

Paratypes - UAPC-ALTA S50947, S52263, S52279, S52268, S52266, S52272, S50989.

Specific diagnosis – Same characters as the genus.

Etymology. The genus is named after the nearby town of Cardston, AB. The specific epithet is proposed in honor of Shayne Tolman of Cardston, Alberta who brought the locality to our attention and spent many hours working with us in the field.

Locality. The locality is 26 km NE of the town of Cardston, Alberta (T5 R254 S12 SE 1/4 W4M; 49° 22' 10" N, 113° 06' 10" W; UTM Grid 12: 5470600N, 347300E).

Stratigraphic occurrence. St. Mary River Formation.

Age. Late Campanian-Early Maastrichtian, Upper Cretaceous.

Results

Of the fifty specimens of this leaf type available, five of these are complete or nearly complete, Morphotype Quality Index = 2 (Leaf Architecture Working Group, 1999). Leaves are simple and ovate to elliptic with an entire margin (figs. 3.2a-c). Several leaves show petioles attached, with the longest segments up to 2 cm long (dictated by the size of the collected block). Petioles show five to seven longitudinal vascular bundles that lack transverse septa (fig. 3.2d). Petiolar attachment is marginal and the petioles are always bent down sharply into the siltstone matrix (figs. 3.2a-d, 3.3e). The leaves likely had long petioles with blades borne at right angles or nearly so to the petiole. Leaf blades are 5-12 cm long and 3.5-8.5 cm wide with a length/width ratio of 1.4:1 (table 3.2). Leaf apices are convex to rounded and the bases are deeply cordate (figs. 3.2a-d, 3.3a, 3.3b).

Venation is campylodromous, with 23-27 primary veins (figs. 3.2a, 3.2b). Five to seven primary veins, enter the base of the leaf, the outermost primaries branching to give rise to the most basal primary veins (figs. 3.2d, 3.3e). The three medial primary veins are more or less parallel to one another for the entire length of the leaf (figs. 3.2a, 3.2b, 3.3c). The outermost primary vein becomes the fimbrial (marginal) vein that dichotomizes several times in the cordate base and gives rise to additional primaries (figs. 3.2d, 3.3d, 3.3e). The outermost primary veins anastomose just beneath the apex of the leaf (figs. 3.2a, 3.3b). All of the remaining primary veins converge around an apical pore (fig. 3.3b).

Secondary veins diverge from the three medial primary veins at angles of 40-45° in most of the leaf blade to 90° near the leaf base (figs. 3.3c, 3.3e). Towards the leaf margin secondary veins typically arise at angles of 90° or nearly so. There are from 10-40 of these secondary ("cross" veins of Golovneva 1997) veins per cm, but 30-35 are common in most of the lamina. Their numbers are greatest near the leaf margin (figs. 3.2d, 3.3c, 3.3d); there are fewer secondary veins near the midrib. In some of the best preserved leaves there appear to be alternating major and minor (thick and thin) secondary veins (figs. 3.3f, 3.3g, 3.3h). This pattern is not always regular, however, and occasionally two thin veins occur between two thick veins (fig. 3.3h). Secondary veins occasionally dichotomize (3.3d, 3.3f) or anastomose (3.3f, 3.3g, 3.3h).

Very few of what might be termed tertiary veins (using the terminology of the Leaf Architecture Working Group 1999) are seen in the fossil leaves. These are distinctly thinner veins that occur at right angles to the secondary veins (figs. 3.3f, 3.3g). In some of the best-preserved leaves there are polygonal patterns preserved on the surface of the fossils that have split between the two leaf surfaces (fig. 3.3i). While these polygonal patterns may represent tertiary venation, when examined closely, these hexagonal patterns overlap with the secondary veins and appear to be superimposed on them (fig. 3.3i). In some parts of the leaf they are preserved in sediment between the two leaf surfaces. It is probable that these patterns are the outlines of underlying aerenchyma due to their shape and position. The thickness of the dark material that outlines the polygonal pattern is about 50 μm, about the size of parenchyma cells.

Russian fossil *Haemanthophyllum* leaves

Haemanthophyllum kamtschaticum Budantsev

Budantsev first described the genus *Haemanthophyllum* in 1983 from the Paleocene-Eocene of western Kamchatka. The holotype of *H. kamtschaticum* Budantsev (generitype) was reexamined here (figs. 3.4a, 3.4b, table 3.1). In addition to the type specimen, two other specimens were examined from the same locality (figs. 3.4c-e). The specimen in fig. 3.4c is illustrated by Budantsev (1983) in the original paper. The other specimen (figs. 3.4d, 3.4e) is from the same locality but not illustrated by Budantsev (1983). In addition to the specimens illustrated here, two other specimens (Budantsev

1983; pl. 63, Figs. 1, 4) were not available for examination. In table 3.1 we show two rows of data for *H. kamtschaticum*; the first is from the original holotype, the second is Budantsev's (1983) concept of the species as shown in Golovneva (1997, Table)

The holotype of *H. kamtschaticum* is a leaf fragment with entire margin, cordate base, fimbrial vein, up to nine recurved primary veins, and 24-35 secondary veins per cm (table 3.1; fig. 3.4a). Note that the number of secondary veins per cm counted by us is markedly higher than the 9-13 originally reported by Budantsev (1983) in the generic description. Secondary veins remain unbranched or dichotomize and/or anastomose between adjacent primary veins (fig. 3.4b). There are certain areas on the holotype where secondary veins show several closely spaced anastomosing dichotomies between the adjacent primaries (fig. 3.4b). No triple midvein is visible (fig. 3.4a). The second specimen Budantsev illustrated has a long, thickened petiole (< 7 cm in length) with multiple veins that continue as a thickened, midvein into the blade (fig. 3.4c). The primary veins branch into the lamina from the midvein with the most basal veins recurving into a cordate base that is slightly concave-convex (fig. 3.4c). No triple midvein is visible (fig. 3.4c). The third leaf fragment studied here (not illustrated by Budantsev) shows a fimbrial vein, dense secondary veins (fig. 3.4d) and possible polygonal aerenchyma between secondary veins (fig. 3.4e).

Haemanthophyllum cordatum Golovneva

Golovneva described *H. cordatum*, from the late Maastrichtian-Danian sediments (Rarytkin Series) of the Koryak Highlands in Russia (Golovneva 1987). The holotype (fig. 3.4f-h) was reexamined, but was difficult to study because the specimen is preserved as a black impression on a black matrix. The leaf has an entire margin, convex to rounded apex, cordate base, and a triple midvein. The number of primary veins appears to be 25, with a fimbrial vein visible in some marginal areas. The margin was not preserved or was slightly degaged away in parts of the specimen making it difficult to trace the path of the outermost veins. Golovneva (1987, Plate I, 1) originally illustrated the outermost primary veins merging with the fimbrial vein; however, we cannot observe the actual leaf margin with certainty in many areas of the specimen. It appears that several of the primary veins do merge together at the apex of the leaf. Golovneva reports 18 secondary veins per cm in this species; we count 7-25 secondaries.

Extant monocot leaves

Leaves of several extant monocots were examined in this study for comparison with the fossil leaves from Cardston (table 3.2). We used taxa from all of the previously published families for which affinities have been suggested (Golovneva 1997) and several others suggested to us (Josef Bogner pers. commun. 2000) as having some similarity in minor venation patterns to our fossil leaves. Illustrations that appear in this paper are only of those leaves that showed the closest similarities to those fossils described here; however, several other taxa appear in table 3.2.

Leaves of *Alisma subcordata* Raf. (Alismataceae) are obovate to elliptical with decurrent bases and convex to acuminate apices (table 3.2). Some leaves show an emarginate apex with an acuminate leaf tip. There are 9 primary veins, the outer two of which merge with the fimbrial vein midway up the leaf. The primary veins do not merge beneath the leaf apex but extend into the tip itself. There are 5-12 secondary veins per cm that do not anastomose but sometimes dichotomize (table 3.2). Secondary veins, all of more or less equal thickness, diverge at angles of 35-45° near the midvein and 70-90° near the leaf margin (table 3.2). Tertiary veins are present and occasionally dichotomize, and they have a wavy or sinuous course in the lamina, often arising at right angles. Golovneva (1994) illustrates similar secondary venation in *A. plantago-aquatica* L. These veins form the irregular, rectangular areoles.

Caldesia Parl. (Alismataceae) leaves (ALTA 49675) were examined from a cultivar growing at the Technischen Hochschule Zürich (figs. 3.5c, 3.5d). They are ovate with cordate bases and acuminate apices, with 13-15 primary veins (fig 3.5c, table 3.2). [Note: *Caldesia parnassifolia* (Bassi ex L.) Parl. (MO 2326418) examined at Missouri Botanical Garden Herbarium had 17 primary veins.] All of the primary veins merge with the fimbrial vein (fig. 3.5c, arrows) except the medial vein that enters the leaf tip. There are 30 secondary veins per cm that arise at angles of 60-70° near the midvein and 90° near the leaf margin. There are major and minor secondary veins that anastomose and dichotomize (fig. 3.5d). Tertiary veins appear to be absent (fig. 3.5d).

We examined 8 different species of *Echinodorus* Rich. ex Engelm. (Alismataceae). Of these *Echinodorus inpai* Rataj, *E. osiris* Rataj, *E. longiscapus* Arech., *E. decumbens* Kasselmann, *E. uruguayensis* Arechavaleta were not put in table 3.2 as they greatly differ from the fossil leaves in having narrow, oblong leaves and very few primary veins. *Echinodorus glaucus* Rataj (Alismataceae) leaves are ovate to oblong with cordate bases and convex to rounded apices (fig. 3.5a, table 3.2). There are 11-13 primary veins, the outermost of which merge with the fimbrial vein (fig. 3.5a, arrows), while the inner three veins enter the leaf tip. There are 6-10 secondary veins per cm diverging at 70-80° near the center of the leaf and 80-90° near the margin (table 3.2). Secondary veins have a curving course and some appear straight or slightly sinusoidal. Major and minor secondary veins occur, show a very irregular course, and can anastomose and dichotomize (table 3.2). Tertiary veins are present; and tertiary and possible quaternary veins form irregular, polygonal areoles.

Leaves of *Echinodorus grandiflorus* (Chamisso *et* Schlectendal) Micheli (Alismataceae) leaves are ovate with cordate bases and convex apices (table 3.2). They have 15-17 primary veins, the outermost of which merge with the fimbrial vein, whereas the inner three extend into the leaf apex (table 3.2). The most basal primary veins are very weak in this taxon but run the same course as the stronger primary veins. There are 8-11 secondary veins per cm diverging at angles of 60° near the midvein and 80-90° near the leaf margin (table 3.2). Secondary veins have a slightly curving course and some are straight or sinusoidal. Major (fig. 3.5b, at x) and minor secondary veins (fig. 3.5b, at 0) are present. The minor secondary veins often show a sinuous course, while the stronger secondary veins have a straighter course (fig. 3.5b). Tertiary veins usually arise perpendicular to secondary veins, often dichotomize, and produce irregular areoles (fig. 3.5b). Quaternary veins do occur but are rare (table 3.2).

Echinodorus subalatus (Mart.) Griseb. (Alismataceae) leaves are ovate with convex bases and straight to slightly convex apices (table 3.2). There are 9 primary veins, the outer three on each side merge with the margin. There are 8-9 secondary veins per cm, which diverge at 50-55° near the center and margins of the leaf. These secondaries are often not straight but run a sinusoidal course in the leaf lamina. Major and minor secondary veins are present, dichotomize frequently, and anastomose occasionally. Minor secondary veins occur irregularly and frequently curve apically, terminating in the above major secondary before reaching the adjacent primary. Tertiary veins are perpendicular, or nearly so, to the secondaries. They have a straight to sinuous course and dichotomize toward the midvein. Fourth order veins are present (table 3.2) and form irregular, rectangular to rarely triangular areolation.

Leaves of *Aponogeton madagascariensis* L. f. (Aponogetonaceae) are oblong to slightly obovate with asymmetrical decurrent bases and emarginate apices (table 3.2). The leaves examined here were submerged and have a fenestrate lamina. There are 13 primary veins, all of which merge with other primary veins from the outside in, but not with, the marginal vein. This anastomosing sequence starts with the outermost primaries merging with adjacent primaries just below the apex continuing admedially. There is a triple midvein that runs the entire length of the lamina. The number of secondary veins per cm is 5-6 (table 3.2). Secondary veins are of uniform thickness, do not anastomose or dichotomize, and diverge at 80-90° near the midvein and the margins. There are no tertiary veins in this species.

Ottelia ulvifolia (Planch.) Walp. (Hydrocharitaceae) has leaves that are oblong, somewhat linear, with cuneate bases and straight apices (table 3.2). All the leaves of this species that we examined were growing submerged. There are 7-19 primary veins the outermost of which merge with the fimbrial vein. The inner primary veins continue to the apex and join in the leaf tip. There are only 3-4 secondary veins per cm (table 3.2). The angle of divergence of secondary veins is 60-90° in the center of the leaf and 60-90° near leaf margins. There are major and minor secondary veins; however, secondary veins rarely anastomose or dichotomize. Third and possible fourth order veins make up rectangular to elongate polygonal areoles, especially near the midvein. Areoles are larger near the midvein and decrease in size toward the leaf margin.

Leaves of *Butomopsis latifolia* (D. Don) Kunth (Limnocharitaceae) are elliptical with cuneate bases and straight to acuminate apices (table 3.2, figs. 3.6e, 3.6g). There are 7-9 primary veins, the outermost of which merge with the adjacent primary vein near the leaf apex (fig. 3.6g). There are 10-12 secondary veins per cm that diverge at angles of 40-50° near the midvein and 80-85° near the margin (table 3.2, figs. 3.6f, 3.6g, 3.6h). Major and minor secondary veins are present (fig. 3.6g). Major secondary veins run a fairly straight course, dichotomize occasionally and anastomose rarely. Minor secondary veins appear irregularly between major secondary veins and run a weak sinusoidal course (fig. 3.6h); these commonly dichotomize and anastomose, with branches occasionally curving toward the leaf apex and terminating in the adjacent secondary. Tertiary veins form well-developed four to many-sided polygonal areoles (fig. 3.6f, 3.6h). Areoles are vertically elongate near the center of the leaf (fig. 3.6f) and horizontally elongate near the leaf margins (fig. 3.6h). *Butomopsis* leaves, like those of *Limnocharis* (below) are fleshy, especially near the center.

Hydrocleys martii Seubert (Limnocharitaceae) leaves are elliptical with cordate bases and rounded apices (table 3.2, fig. 3.5e). There are 11 primary veins that continue to the apex but do not merge with adjacent primaries or the fimbrial vein (fig. 3.5e, table 3.2). Leaves show a triple midvein (fig. 3.5f). The two lateral primaries thin toward the leaf apex and do not reach the apex. One leaf showed two primaries anastomosing beneath the apex (fig. 3.5e, arrow). The primary veins merge at the apex forming an apical ring (fig. 3.5e). There are 6-20 secondary veins per cm (far fewer secondary veins near the midrib) that arise at angles of 70° near the midvein and 90° at the margin (table 3.2). Major and minor secondary veins are present (table 3.2), and both are more or less straight. Tertiary veins are mostly perpendicular to the secondary veins and form regular, polygonal areoles that are elongated vertically near the midrib (fig. 3.5f) and horizontally near the leaf margins. There are no quaternary veins.

Leaves of *Limnocharis flava* (L.) Buchenau (Limnocharitaceae) are elliptical with cordate bases and rounded apices (figs. 3.5g, 3.5h). There are 11-13 primary veins, 10-12 of which merge with adjacent primaries near the apex (normally within one millimeter of the apex). The midvein is the only primary vein that does not merge with other primaries. The primary veins do not merge with the fimbrial vein. There are 11-13 secondary veins per cm that diverge at angles of 60-80° near the midline and 90° near the margin. Major and minor secondary veins are present and consistently alternate with each other. The major secondary veins run a straight course and occasionally dichotomize but do not appear to anastomose (fig. 3.5h). The minor secondary veins regularly dichotomize and anastomose running a weak sinusoidal course (fig. 3.5h). Tertiary veins are present and frequently dichotomize and anastomose (fig. 3.5h) forming a network of polygonal areoles that appear to be concentrated on the adaxial side of the leaf lamina. Near the center of the leaf on the abaxial surface is another series of veins forming regular, polygonal, reticulate areoles. In herbarium specimens it is necessary to use both transmitted and reflected light of various intensities in order to see these vein patterns clearly. Leaves of *L. flava* are fleshy and full of aerenchyma, especially near the center.

Limnocharis laforestii Duchessaing (Limnocharitaceae) leaves are oblong with cuneate bases and acuminate apices (figs. 3.6a, 3.6c, table 3.2). There are 11–13 primary veins with the three adjacent primary veins on each side of the 'triple' midvein merging near the apex (figs. 3.6a, 3.6b, 3.6c). The primary veins do not merge with the margin. The 'triple' midvein appears to be composed of two weak primary veins that run adjacent to the midvein (fig. 3.6b) that thin distally and do not reach the apex (fig. 3.6c). There are 8-11 secondary veins per cm that diverge at angles of 65-75° near the midvein (fig. 3.6c) and 75-90° near the margin (fig. 3.6d, table 3.2). Major and minor secondary veins regularly alternate and run straight to slightly sinusoidal courses while occasionally dichotomizing but rarely anastomosing (fig. 3.6c). Tertiary veins appear random reticulate, i.e., they anastomose (rejoin) with other tertiary or secondary veins at random angles (Leaf Architecture Working Group 1999) forming well-developed polygonal areoles (fig. 3.6b, 3.6d). As in *L. flava* there is a second set of overlapping regular, polygonal, reticulate veins in the center of the leaf near the abaxial leaf surface (fig. 3.6d). These veins arise from the primary and secondary veins. Quaternary veins are present forming freely ending veinlets that appear unbranched and one-branched (fig. 3.6d).

Leaves of *Potamogeton lucens* L. (Potamogetonaceae) are elliptical with decurrent bases and acuminate to convex apices (table 3.1). There are 9 primary veins that merge with adjacent primaries near the leaf apex. There is a single midvein, and the adjacent primaries are widely spaced from this medial vein. This species shows minute serrations at the leaf margin and a distinct fimbrial vein. Other species have been described with clearly serrate teeth (e.g., *P. crispus* L.) or what appear to be entire margins with serrations that are not visible to the naked eye (e.g., *P. perfoliatus* L.) (Cook 1996b). Primary veins do not merge with the fimbrial vein (table 3.1). The number of secondary veins per cm is only 6-10 and the angles of divergence of the secondaries are 40-60° near the midvein and 60-80° near the leaf margin (table 3.1). There are no major and minor secondary veins. Secondary veins often anastomose and dichotomize and distinct tertiary veins occur at right angles to the secondary veins. They often show a sinuous course in between secondary veins, but always attach perpendicular to the adjacent secondary vein. Tertiary veins also rarely dichotomize.

Haemanthus katherinae Baker (Amaryllidaceae) leaves are generally oblong with cuneate bases and acuminate tips (table 3.1). There are 21 primary veins that do not merge with the fimbrial vein and many of the primary veins merge near the leaf apex. There are 11-23 secondary veins per cm with an angle of divergence of 60° near the center, increasing to 80° near the margin. Secondary veins often dichotomize and sometimes anastomose. There is a common occurrence of what could be termed "intersecondary veins" (Leaf Architecture Working Group 1999) that do not reach the adjacent primary or the margin. These are slightly thinner than the normal secondary veins and they usually end blindly. *Haemanthus* leaves also do not show a regular alternation of thin and thick secondary veins. Occasional slightly thinner veins continue between the adjacent primary veins, but these are rare. Regular tertiary veins occur rarely (table 3.1).

Stemona tuberosa Lour. (Stemonaceae) have ovate leaves with cordate bases and acuminate tips (table 3.1). There are 11 primary veins; the outer three on each side merge with the leaf margin. These primary veins continue along the margin and then end in the margin. The outer primaries do not merge with each other at the margin but disappear prior to reaching the leaf apex. There is a single medial primary vein, and the adjacent primaries are widely spaced from this medial vein. These four adjacent primaries continue to the apex of the leaf and enter the acuminate tip without merging. The number of secondary veins per cm is 28-30, and the angles of divergence of secondary veins are 90° both in the center of the leaf and near the leaf margin (table 3.1). There appear to be major and minor secondary veins in regular alternation between adjacent primaries. These secondary veins can dichotomize and anastomose. No tertiary veins were observed (table 3.1).

Discussion

Comparison with fossil leaves

An entire margin, parallel petiolar veins, and campylodromous primary venation (Leaf Architecture Working Group 1999) of the fossil leaves from Cardston indicate that this plant is a monocotyledon. The ovate blade with a large number of primary veins originating at or near the leaf base and converging at or near the apex, dense secondary veins and thin, higher order veins forming polygonal areolae (Golovneva 1997) are similar to those in leaves described as *Haemanthophyllum* Budantsev (1983). Budantsev (1983) erected *Haemanthophyllum* based on 20 fossil leaves collected from several localities in Kamchatka, Russia. These localities range in age from Late Paleocene/Early Eocene (Anadyrka Formation) to Middle to Late Eocene (Tkaprorayam Formation). The specimens Budantsev illustrated, and the one that we studied that he did not illustrate, were incomplete fragments. From these fragments of apices, bases and margins of different ages, Budantsev constructed the concept of the genus *Haemanthophyllum* (1983). Subsequent authors placed other species of varying geologic ages and localities in this genus due to morphological similarities (table 3.1). This resulted in a diverse array of taxa being assigned to *Haemanthophyllum* based upon a questionable association of leaf parts.

Five species of *Haemanthophyllum* are currently recognized by Golovneva (1997): *H. kamtschaticum* Budantsev, *H. zhilinii* (Pneva) Golovneva, *H. nordenskioldii* (Heer) Boulter et Kvaček, *H. cordatum* Golovneva, and *Haemanthophyllum* sp. from Ireland (table 3.1). The remaining species assigned to *Haemanthophyllum* resemble *H. kamtschaticum* (table 3.1 - *Haemanthophyllum*. Sp. 3 & 5) or *H. nordenskioldii* (table 3.1- *Haemanthophyllum*. Sp. 1 & 4) (Golovneva 2000).

The holotype for *H. kamtschaticum* is a fragment of one lobe of a cordate base from the Anadyrka Formation of the Late Paleocene/Early Eocene (figs. 3.4a, 3.4b, 3.4d). The thickness, branching pattern and density of the primary and secondary veins are similar to our leaves; however, without an attached apex, midrib or petiole, it is difficult to compare *H. kamtschaticum* to our leaves morphologically. The second fragmentary base with a petiole from the same locality, assigned to *H. kamtschaticum* (Budantsev 1983), is also without an apex and most of the lamina (fig. 3.4c). The primary veins are barely visible but they appear fewer in number, and the angle at which they recurve is shallower than in the holotype specimen. An illustration of the secondary veins of this specimen appears in Golovneva (1997, Fig. 2a). However we were unable to observe the secondary veins in the actual specimen. Because of the state of preservation it is not possible to determine that the holotype and this second specimen belong to the same taxon.

The remaining leaf fragments illustrated by Budantsev (1983, Plate 63, Figs. 1 & 4) and Golovneva (1997, Fig. 2b-d) are from localities within the Tkaprovayam Formation that are younger (Middle to Late Eocene) than the previously discussed specimens from the Anadyrka Formation. These specimens are also unconnected leaf fragments of varying shape with a fimbrial vein, and numerous primary and secondary veins (Budantsev 1983; Golovneva 1997). The fragmentary nature of the specimens, locality and age differences preclude the assignment of these specimens to *H. kamtschaticum*. We propose that the genus *Haemanthophyllum* be reserved for fragments of leaf bases resembling the holotype and that the remaining leaf fragments assigned to this species be reexamined for affinities once more complete leaves are discovered.

Leaf fragments from three different localities (Ashutas Mountain, Zhayremsk Quarry, and Kinyak) and similar ages (Late Oligocene to Early Miocene) from Kazakhstan have been assumed to represent a single species, *H. zhilinii* (Golovneva

1997). Previous workers have assigned fragmentary specimens from Ashutas Mountain to *Alisma macrophylla* Heer (Kryshtofovich 1956) and *Aponogeton zhilinii* Pneva (1988). Zhilin (1974) described a small laminar fragment from Kinyak as *Aponogeton* Pneva sp. (1988) later included this small fragment in *Aponogeton zhilinii*. All of this illustrated material shows some similarities in primary and secondary venation and density to *Haemanthophyllum* and certain specimens appear similar to *H. kamtschaticum* (Golovneva 1997, Figs. 5a & 5c). However, the fragmentary nature of the material and lack of clear morphological characters (i.e., laminar characters, base and apex shape and overall leaf size) leave their taxonomic affinities in doubt.

Golovneva, after reexamining Heer's specimens in Stockholm, suggests that leaf specimens from the early Paleocene Barentsburg Formation and the Eocene Skilvika Formation of Spitsbergen be assigned to *H. nordenskioldii* (Heer) Boulter et Kvaček (Golovneva 1997; table 3.1). Heer (1868) originally assigned fragmentary specimens from the Barentsberg Formation (Heer 1868, Plate 30, Figs. 1b, 5b, 6a, 7; Golovneva 1997, Fig. 1b) and several fragmentary specimens from the Skilvika Formation (Heer 1876, Plate 27, Figs. 1-3a) to *Potamogeton nordenskioldii* based on small laminae (relative to *Alisma macrophylla*) and convex (blunt) apices. He assigned the remaining specimens from the Skilvika Formation to *Alisma macrophylla* based on large laminae and acuminate leaf tips (Heer 1876, Plate 26, Figs. 1-6; Plate 27, Figs. 3b, 3c, 4-7; Golovneva 1997, Figs. 1a, 1c). Golovneva (1997) suggested that both leaf types belong to the same species of *Haemanthophyllum* [now called *H. nordenskioldii* (Heer) Boulter et Kvaček]. However, the assignment of these fragmentary plant remains of varying morphology and age to *Haemanthophyllum* is tenuous. In addition, these leaves from Spitsbergen, unlike our leaves, have larger laminae, cuneate bases, attenuate to convex apices, lack a triple midvein in the leaf base, and have only 7-9 cross veins per cm (table 3.1).

Boulter and Kvaček (1989, Figs. 22D, E; table 3.1 - *Haemanthophyllum* sp. 2) originally assigned fragmentary specimens with narrow oblong leaves and parallelodromous primary venation from the Late Paleocene/Early Eocene of Ireland to *H. nordenskioldii.* Golovneva (1997) concluded that the leaf characters were sufficiently different from the Spitsbergen material and recommended that they be removed from *H. nordenskioldii*, but recognized that they may represent a new species of *Haemanthophyllum* (Golovneva 1997; and L.B Golovneva 1999 pers. commun.). Again, without an apex or base it is difficult to classify the Irish material. The Irish leaves are differ in morphology from the Cardston leaves, but resemble fragmentary remains described by Zhilin (1974) as *Aponogeton tertiarius* Zhil. and may show affinities to extant Aponogetonaceae or Potamogetonaceae.

Other leaf fragments sometimes assigned to *Haemanthophyllum* include a specimen with a strong triple midvein, representing the middle to basal part of a leaf from the Early Paleocene of the Tsagajan Formation in the Amur Region of Russia. This leaf appears similar to specimens described as *H. nordenskioldii* (Krassilov 1976, Plate 11, Figs. 3, 4; table 3.1 - *Haemanthophyllum* sp. 1). The specimen is fragmentary, lacking an apex and base (Golovneva 1997, suggests the base is cuneate). The secondary veins appear to be as numerous as 25 per cm, slightly greater than the 14-17 reported by

Golovneva (1997), and diverge at nearly 90° near the midvein. The difference in the angle of divergence of secondary veins and the lack of a cordate base with recurved primary veins, distinguish these specimens from the Cardston leaves.

There are several known occurrences of *Haemanthophyllum*-like leaves from North America (table 3.1). Brown (1962, Pl. 15, Figs. 1, 4, 6) described fragmentary specimens of monocot leaves with large blades from the Paleocene Fort Union Formation in North and South Dakota as *Alismaphyllites grandifolius* (Penhallow) Brown. These leaves from two different localities were combined by Golovneva (1997, Table) and described as *Haemanthophyllum* sp. 3. An acuminate leaf apex, described as an unidentified monocot by McIver and Basinger (1993) from the Paleocene Ravenscrag Formation of Saskatchewan, Canada, has been referred to as *Haemanthophyllum* sp. 5 by Golovneva (1997; table 3.1). Two leaf fragments also similar to *Haemanthophyllum* have been described from the Paleocene Sagavanirktok Formation of northern Alaska (Spicer et al. 1994). One is a fragmentary cuneate leaf base (Spicer et al. 1994, Fig. 3.2); the other is a fragment of a rounded apex (Spicer et al. 1994, Fig. 3.3). These specimens are referred to as *Haemanthophyllum* sp. 4 (Golovneva 1997; table 3.1). It is quite possible that these are fragments of two different taxa. All of these specimens are too poorly known to assign them with certainty to *Haemanthophyllum*, or the fossil leaves described in this paper, and are in need of reinvestigation once more specimens are found.

The Cardston fossil leaves are most similar to *H. cordatum* (Golovneva 1987). The overall shape, size, number of primary veins, merging of several primary veins below the apex, and angles of divergence of secondary veins are similar; however, there are several notable differences. Golovneva (1987, Fig. 1) illustrated the outermost primary veins merging with the margin. In the Cardston leaves the primary veins continue to the apex without merging with the margin. This is a key character that distinguishes the Russian specimens from our material. An apical pore is present in the Cardston leaves, but due to poor preservation its presence or absence is unknown in the Russian material. A larger number of secondary veins per cm is seen in the Cardston leaves (up to 40) than in *H. cordatum* (13-18). Even considering variability in preservation and our counts of 7-25 veins per cm on the holotype specimen, it appears that the secondary veins have a greater density in the Cardston leaves (table 3.1). In addition to these morphological differences the Cardston leaves are older than those of *H. cordatum* by at least 5 million years, based on Russian stratigraphy (table 3.1).

Comparison with extant monocots

Budantsev (1983) based the name *Haemanthophyllum* on similarities of the fossil leaves to leaves of *Haemanthus* L. (Amaryllidaceae). Several workers concluded that these leaves were more closely related to *Aponogeton* (Zhilin 1974; Golovneva 1987, 1997; Pneva, 1988; Boulter and Kvaček 1989) or *Potamogeton* (Heer 1868,1876; Krassilov 1976; Boulter and Kvaček 1989). Heer (1876), Krystofovich (1956), Brown (1962), and Golovneva (1997) also compared fossil leaf fragments to those of Alismataceae. Our comparisons include Hydrocharitaceae, Limnocharitaceae, and Stemonaceae (table 3.2).

Fossil leaves from Cardston differ from those of *Haemanthus* in general leaf shape. While *Haemanthus* leaves are oblong with cuneate bases and acuminate tips, those of the fossil are ovate with cordate bases and convex to rounded apices. A number of characters are, however, shared by these two taxa, including the number of primary veins and primary veins that merge near the leaf apex and not with the margin. The number of secondary veins per cm overlap between these two taxa, but the fossil leaves have greater numbers of secondary veins per cm, especially near the margin. The angles of divergence of the secondary veins are similar; however, angles near the center in the fossil leaves can be more acute (table 3.2). The fossil leaves show regular major and minor secondary veins. Minor secondary veins in *Haemanthus* are rare. The midvein in *Haemanthus* is undulating, unlike that seen in the fossil leaves. Secondary veins in *Haemanthus* may dichotomize and anastomose as in the fossil leaves, but common intersecondary veins (Leaf Architecture Working Group 1999) occur in this genus. These do not occur in the fossil leaves. Tertiary veins occur rarely in *Haemanthus* leaves, but these are much more common in the fossil leaves from Cardston.

Leaves of *Stemona* are ovate with cordate bases like those of the fossil, but with acuminate apices, rather than convex to rounded, as in the fossils (table 3.2). The number of primary veins is small (11) compared to the 23-27 veins seen in the fossil leaves. The primary veins in *Stemona* reach the margin and extend part way up the leaf in the margin (becoming what might be considered a fimbrial vein). However, in *Stemona* the primary veins never merge in the margin. The lowermost primary disappears just as the inner adjacent primary vein approaches the margin and continues toward the apex acting as a fimbrial vein. The number of secondary veins per cm is comparable between *Stemona* and *Cardstonia*, and their angles of divergence near the margin are both 90°. However, leaves of *Stemona* show angles of 90° throughout the leaf, even near the midvein, while those of the fossil leaves are 45-60° near the center of the leaf. The secondary veins are similar to those of *Cardstonia* with regular alternation of major and minor secondaries that dichotomize and anastomose. Tertiary veins, however, were not observed in leaves of *S. tuberosa.*

Leaves of *Potamogeton lucens* are elliptic with decurrent bases and acuminate to convex tips. Leaf shape in the family Potamogetonaceae is highly variable and often heteromorphic, with floating leaves that are broad and petiolate and submerged leaves very thin to lanceolate or elliptic (Cook 1996a). There are about 80-90 species of *Potamogeton*, some of which show minute teeth and serrated margins (Cook 1996b). The number of primary veins, however, is much smaller than in the fossil leaves described here (table 3.2). These primaries, like those in *Cardstonia* leaves, do not merge with a fimbrial vein but continue to the leaf apex. The number of secondary veins per cm in *P. lucens* is very small and there are no minor secondary veins. In addition, the tertiary veins in *P. lucens* diverge at right angles and show a sinuous course between secondary veins; they rarely dichotomize.

Van Bruggen (1990) studied *Aponogeton* leaves in some detail. We examined *A. madagascariensis* (table 3.1) and *A. ulvaceous* in this study. *Aponogeton* leaves are more oblong (linear) than those of the Cardston fossil taxon. While *A. madagascariensis* has a decurrent base, the shape can vary in *Aponogeton* with some species (e.g., *A. cordatus* Jumelle) developing a shallow cordate base (van Bruggen 1990). The fossil leaves have deeply cordate bases with lobes that extend for some distance below the point of petiolar attachment, unlike any extant species of *Aponogeton*. The leaf apex shape in *Aponogeton* can be straight, convex, rounded, and emarginate (van Bruggen 1990). The fossil leaves show convex to rounded apices that are similar to some *Aponogeton* species, e.g., *A. jacobsenii* van Bruggen (van Bruggen 1990).

The thirteen primary veins in *A. madagascariensis* are significantly fewer than the 23-27 observed in the fossil leaves. This is also consistent with the typical 11-15 primary veins reported by Tomlinson (1982) for the genus *Aponogeton*. The primary veins do not merge with the fimbrial vein but do merge with adjacent primaries in *Aponogeton* and *Cardstonia* leaves. In *Aponogeton*, the first veins to merge near the apex are the outermost pair of primary veins, each of which merges with an adjacent primary. This pattern continues until most of the primaries join at the leaf apex. Although adjacent primaries do occasionally merge in the fossil leaves, there does not appear to be a successive admedial pattern of merger as seen in *Aponogeton*. The number of secondary veins per cm is 5-6 in *A. madagascariensis* while the Cardston fossil leaves show a much greater density (10-40). Secondary veins diverge at angles of 80-90° in *A. madagascariensis* at the center and margins of the leaf while those in *Cardstonia* leaves diverge at angles of 45-60° in the center and 90° at the margins. *Aponogeton* leaves lack major and minor secondary veins, whereas there is a consistent alternation of major and minor veins in the fossil leaves. Although secondary veins are not seen dichotomizing or anastomosing in *A. madagascariensis*, they do dichotomize or anastomose occasionally in *A. madagascariensis* var. *henkelianus* (van Bruggen 1990). Third order veins are normally absent in submerged leaves of *Aponogeton* (Tomlinson 1982), but can form well-developed regular areoles in emergent leaves, e.g., *A. junceus* Lehm. (=*A. spathaceum* E. Meyer). Third order veins in the Cardston fossil leaves are few in number and form irregular areoles, unlike those of *Aponogeton*. An apical pore, as in the Cardston fossil leaves, has been reported in old leaves of *Aponogeton* (Tomlinson 1982).

Leaves of *Ottelia ulvifolia* (Hydrocharitaceae) differ in overall leaf shape from the ovate leaves from Cardston (with cordate bases and convex to rounded apices) in being oblong to linear with cuneate bases and straight apices. The genus *Ottelia* Pers. contains about 21 species (Cook 1996a), however; and cordate bases have been reported in some taxa (Tomlinson 1982). There are fewer primary veins (7-19) than in *Cardstonia*, and the outer veins in *O. ulvifolia* merge with the margin. There are fewer secondary veins per cm (3-4) than the 10-40 seen in the Cardston leaves. Angles of divergence of secondary veins can overlap, and major and minor secondary veins occur in both (table 3.2); however, secondary veins rarely anastomose or dichotomize as they do in the Cardston fossil leaves. The rectangular to elongate polygonal areoles that are formed by third and fourth order veins in *O. ulvifolia* are absent in the Cardston leaves.

The Cardston fossil leaves are more similar to those of Alismataceae and Limnocharitaceae than to leaves of any of the other families examined here. Ovate leaf shapes with cordate bases occur in Alismataceae, as in *Cardstonia* (Meyer 1935a; table 3.2). Leaves of *Alisma* differ in leaf base shape, lack of major and minor secondary veins, and the secondary veins do not anastomose (Golovneva 1994; table 3.2). Those of *Caldesia* have more acuminate tips and lack tertiary veins (Mayr 1943; table 3.2). Apices can be convex to rounded in *Alisma* and some *Echinodorus* species similar to the fossil leaves. There are fewer primary veins in Alismataceae (9-15) than in the fossils that show 23-27 veins. In all the Alismataceae examined, the outer primary veins merge with the fimbrial vein. In the fossil leaves all primary veins continue to the leaf apex before fusing. The number of secondary veins per cm is far fewer in most taxa of Alismataceae; however, *Echinodorus* species and *Alisma* can reach the lower limits seen in the fossils. Secondary venation in *Caldesia* is very similar to that in the fossil leaves. Secondary veins in *Echinodorus* have a more curved course in the leaf than those seen in the fossils. The species of *Echinodorus* that we examined have fourth order veins and the areoles formed by tertiary and sometimes quaternary veins are vertically elongate, unlike the horizontally elongate areoles in the fossil leaves. "Weakly developed" apical pores have been reported in older leaves of *Echinodorus* (Tomlinson 1982), but were not observed by us in any of the leaves that we examined. Internal aerenchyma tissues have been described in this family by Meyer (1934, 1935b) and Stant (1964); and large lacunae are present in the leaf mid-rib with much smaller air spaces in the lateral laminae.

The fossil leaves from Cardston show the greatest similarities to those of Limnocharitaceae. *Hydrocleys* has leaves that are nearly ovate to suborbicular (Stant 1967; Cook 1996a). In "dicot" leaf terminology (Leaf Architecture Working Group 1999) the leaf illustrated in fig. 3.5e is classed as elliptic. Bases are cordate as in the fossil leaves (Stant 1967). The number of primary veins is only 11 in *Hydrocleys*, compared to 23-27 in *Cardstonia*. The primary veins do not merge with the fimbrial vein but do merge with other primary veins near the leaf apex as in *Cardstonia*. These leaves show a triple midvein as in *Cardstonia*, but the two lateral veins do not reach the leaf apex. The number of secondary veins per cm overlaps that seen in the Cardston leaves, but never reaches the 40 per cm maximum seen in the fossils. Angles of divergence of secondary veins are similar to those in the Cardston leaves but generally greater near the center of the leaf. Major and minor secondary veins are present that anastomose and dichotomize as in the fossils, and the secondary veins also have a more or less straight course. The tertiary veins in *Hydrocleys* arise at nearly right angles from the secondary veins and there is much more regular areolation than in the fossils. There is an apical pore in *Hydrocleys*, as in *Cardstonia* (Stant 1967).

Leaves of *Butomopsis* are elliptical with cuneate bases, straight to acuminate apices, and are markedly different in shape than leaves from Cardston (table 3.2, fig. 3.6e). The number of primary veins in *B. latifolia* is only 7-9, the lowest count for the family, and more similar to some Alismataceae than the fossil leaves. These primary veins, like those in the fossils and other Limnocharitaceae, do not merge with the margin but merge at or near the apex. Angles of divergence of secondary veins are very similar to those of the fossil leaves. Major and minor secondary veins with a more or less straight course that dichotomize and anastomose (although rarely) are similar to the Cardston leaves. Tertiary veins form somewhat irregular but well-developed polygonal areoles. As in *Hydrocleys* the areoles are more elongate toward the center of the leaf than the margins.

Limnocharis laforestii leaves are oblong with cuneate bases and acuminate apices and therefore differ in general shape from the Cardston leaves (table 3.2). As in *Hydrocleys* there are 11-13 primary veins that do not merge with the margin and a triple midvein is seen near the leaf base, but the two lateral veins do not reach the leaf apex. The number of secondary veins per cm (8-11) overlaps the minimal number seen in the fossil leaves (table 3.2). Angles of divergence of secondary veins are similar to those seen in the fossil leaves but generally greater near the center of the leaf. Major and minor secondary veins that run nearly straight are similar to those seen in the Cardston leaves. These leaves, however, have randomly reticulate tertiary veins with well-developed polygonal areoles, unlike the irregular areolation seen in *Cardstonia*. Quaternary veins also occur in this species. These form freely ending veinlets, like those reported in "dicot" leaves (Leaf Architecture Working Group 1999), and unlike those seen in any of the other monocot taxa observed by us.

Leaves of *Limnocharis flava* show the closest similarities to the Cardston fossil leaves in many characters. The general leaf shape with a cordate base and rounded apex are similar between the two. While the number of primary veins is only 11-13 in *L. flava*, the primary veins do not merge with the fimbrial vein, but do merge with other primary veins beneath the apex, and an apical pore is present (Stant 1967). The angles of divergence of the secondary veins are very similar, while slightly higher in the center of the leaf than in the Cardston fossils (table 3.2). The number of secondary veins per cm in *L. flava* is at the low end for *Cardstonia*. Tertiary veins are very similar to those in the Cardston leaves and they frequently dichotomize and anastomose. Irregular polygonal areolae are present in *L. flava* on the adaxial surface, similar to those seen in *Cardstonia*.

In all leaves examined of Limnocharitaceae we observed internal patterns of aerenchyma. These leaves are especially fleshy near the leaf center whereas the fossil leaves seem to be fleshy throughout. In all extant Limnocharitaceae there appears to be a set of tertiary veins that form larger areoles on the abaxial surface of the leaf. These veins are not seen in reflected light when adaxial leaf surfaces are examined. They are best seen with a combination of transmitted and reflected light on a dissecting microscope. Illustrations of venation of *Butomopsis* (fig. 3.6h), *Limnocharis laforestii* (fig. 3.6d), *Hydrocleys* (fig. 3.5h) are photographed in this type of light. It is difficult to see through the paper on herbarium sheets, and this type of examination of leaf venation is best done on pressed leaves that are not mounted on sheets. The photograph of *Limnocharis flava* (fig. 3.5h) was taken with a predominance of reflected light. In all of these leaves there is an abaxial set of tertiary veins that can be seen to connect to the secondary veins in several places. If these leaves were found as fossils, the predominant pattern seen would depend on how the specimen was cracked open and how close the fracture is to each surface. I illustrate a similar tertiary vein pattern (fig. 3.4e) in the *Haemanthophyllum* sp. fragment from the type locality (one of the specimens collected by Budantsev).

It should be noted that some authors might be observing internal aerenchyma patterns as well as a second set of tertiary veins in fossil leaves. Observations of the leaves of "*Haemanthophyllum*" in the fossil record have had various interpretations of tertiary venation. Golovneva (1997, Pl. 9, Fig. 8) illustrates small polygonal areolae in *H. kamtschaticum* and we show similar features in the Cardston leaves (fig 3.3i). We are interpreting these polygons that can overlap veins (fig. 3.3i, arrows) as aerenchyma. In some fossil specimens it may be extremely difficult to tell whether the patterns observed are underlying aerenchyma, or tertiary venation patterns, or both. The regularity of the nearly hexagonal aerenchyma, if preserved, and its overlap with overlying veins are seen when there is good fossil preservation. Furthermore, the size ranges of the cells surrounding the lacunae are about 50 µm, a reasonable size for parenchyma cells.

While the fossil leaves from Cardston described here have similar numbers of primary veins to those of the genus *Haemanthus*, their overall venation patterns are most like leaves in Alismataceae and Limnocharitaceae. The merging of primary veins with the fimbrial vein in most Alismataceae is a major difference in leaf architecture. Thus, the fossil leaves are most similar to those of Limnocharitaceae in overall vein patterns and the presence of an apical pore where the primary veins converge and unite (Sauvageau 1891, 1893; Stant 1967). Within Limnocharitaceae, *Limnocharis flava* shows the closest venation pattern, even to the order of tertiary veins, to the leaves from Cardston.

The Cardston leaves are unique in the large number of primary veins, the triple midvein that is continuous to the leaf apex, and the irregular areolae formed by tertiary veins. There are few secondary veins in the midrib region, while the number dramatically increases toward the leaf margin. Thus, the Cardston leaves are described as *Cardstonia tolmanii* sp. nov., and we have included them in the Limnocharitaceae.

Limnocharitaceae have often been included in Butomaceae, but a number of characters have suggested a relationship to Alismataceae (Cronquist 1981). In cladistic analyses Limnocharitaceae and Alismataceae form a clade, with Butomaceae either as the sister group or as the basal member of the sister group (Haynes and Holm-Nielsen 1992, Les and Haynes 1995; Les et al. 1997; Soros and Les 2001, 2002). Morphological cladistic analyses (Haynes and Holm-Nielsen 1992) suggest that Limnocharitaceae and Alismataceae may be sister groups, or that Alismataceae are nested within Limnocharitaceae (Haynes and Holm-Nielsen 1992). In molecular studies using *rbc*L Limnocharitaceae is embedded within Alismataceae, suggesting that Alismataceae may be paraphyletic (Les et al. 1997). Data from the internal transcribed spacers (ITS-1; ITS-2) of the nuclear ribosomal region, *rbc*L, the flanking introns and coding region of chloroplast *matK*, and morphology all indicate a sister relationship between Alismataceae and Limnocharitaceae (Soros and Les 2001 2002).

Our reinvestigation of the genus *Haemanthophyllum* suggests that this genus should probably be restricted to leaf fragments that show cordate bases with similar venation patterns to the type. Budantsev's (1983) type specimen is incomplete. As is seen in this study, if only leaf bases were known, leaves of this type might be mistaken for those of *Stemona* or *Caldesia* that show similar secondary vein characteristics. However, when whole leaves are found these may prove to have other affinities. The suggestion that some leaves that have been described as *Haemanthophyllum* are more similar to *Aponogeton* is a valid one (Golovneva 1997). However, the Cardston material is clearly different from Aponogetonaceae in several characters. It becomes evident that most of the previously described species of *Haemanthophyllum* should be reexamined, and larger numbers of more complete specimens are needed from each particular locality before descriptions are made. At the Cardston locality we have a second broad-leaved monocot type that is elliptic with a rounded base and distinctly different tertiary venation pattern from that seen in *Cardstonia* that will be the subject of another study.

The present study also points out the need for a monocot leaf venation terminology. The Manual of Leaf Architecture (Leaf Architecture Working Group 1999) covers "dicotyledonous" leaves and net-veined monocotyledonous angiosperms. However, we ran into several problems in using these terms for the monocot leaves described in this paper. While primary vein terminology will work with these leaves, terminology for secondary and tertiary vein patterns is more problematical. We have tried to describe these patterns in several ways and to use the dicot terminology when possible. However, the distinctions between different leaf venation patterns are not always seen in table format using these "dicot" terms, even though we can distinguish the leaves qualitatively. It is hoped that a terminology will be developed for monocot leaves in the future to aid in descriptions by paleobotanists and neobotanists.

The St. Mary River Reservoir locality near Cardston, Alberta has yielded a large number of extremely well preserved broad-leaved monocots in fine-grained sediments. This remarkable preservation has provided detailed data on the leaf architecture of many taxa including aerenchyma patterns and internal anatomy in some rhizomes. Many plants are also buried *in situ*, providing insights into the ancient habitats and environments of the fossil taxa at the time of deposition. Further work at this site will provide a better understanding of the diversity of these ancient aquatic communities and their paleoenvironment.

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Figure 3.1

Figure. 3.1. Locality.

Figure 3.1. Aerial photo of collecting locality in southern Alberta, Canada. Photo shows St. Mary Reservoir (R), associated dam (D) and both spillways. Locations of two fossil sites along banks of St. Mary River (arrows). Scale bar = 300 m.

Figure 3.1

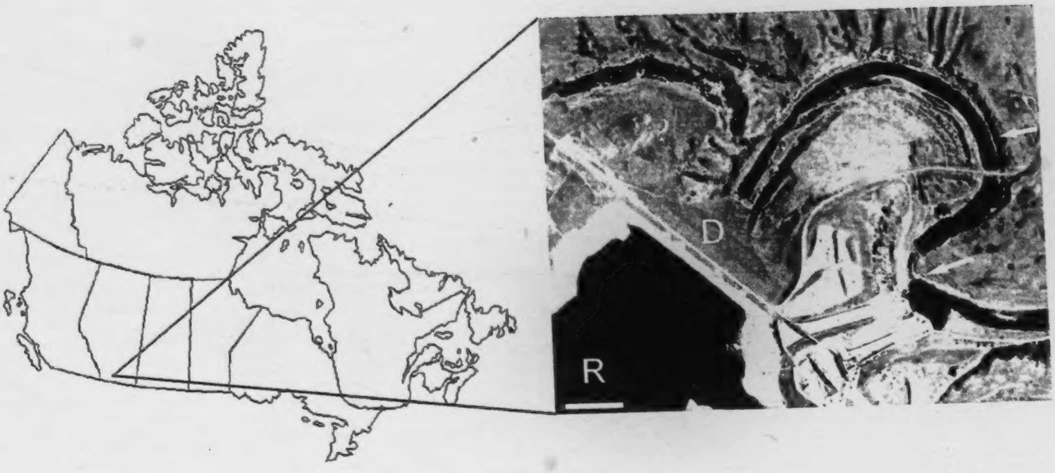

Figure 3.2

Figure 3.2a-3.2d. *Cardstonia tolmanii* Riley et Stockey leaves.

Figure 3.2a. Holotype showing entire margin, rounded apex, cordate base, and triple midvein. All primary veins appear to diminish in thickness toward apex. Note primary veins recurved in base and continuing to apex without merging with marginal vein. Overlapping lobes of the lamina (arrow) are probably an artifact of deposition. Scale bar = 0.5 cm. Holotype S55138A.

Figure 3.2b. Large lamina showing entire margin, cordate base with single lobe, and triple midvein. Note steep angle of divergence of secondary veins near midvein and marginal vein dichotomizing in base (arrow) giving rise to additional primary veins; possible herbivory (*). Scale bar = 0.5 cm. S52263A.

Figure 3.2c. Large lamina showing petiole/lamina interface descending into matrix between cordate lobes. Note basally thickened primary veins on each side of triple mid-vein; arrow indicates dichotomy of primary midvein. Scale bar = 0.5 cm. S50947A.

Figure 3.2d. Cordate base showing petiole descending into matrix at 30°, recurved primary veins radiating near petiole/lamina interface, and large number of secondary veins per cm. Note marginal vein dichotomizing and giving rise to primary veins (arrows). Scale bar = 0.5 cm. S52279A.

Figure 3.2

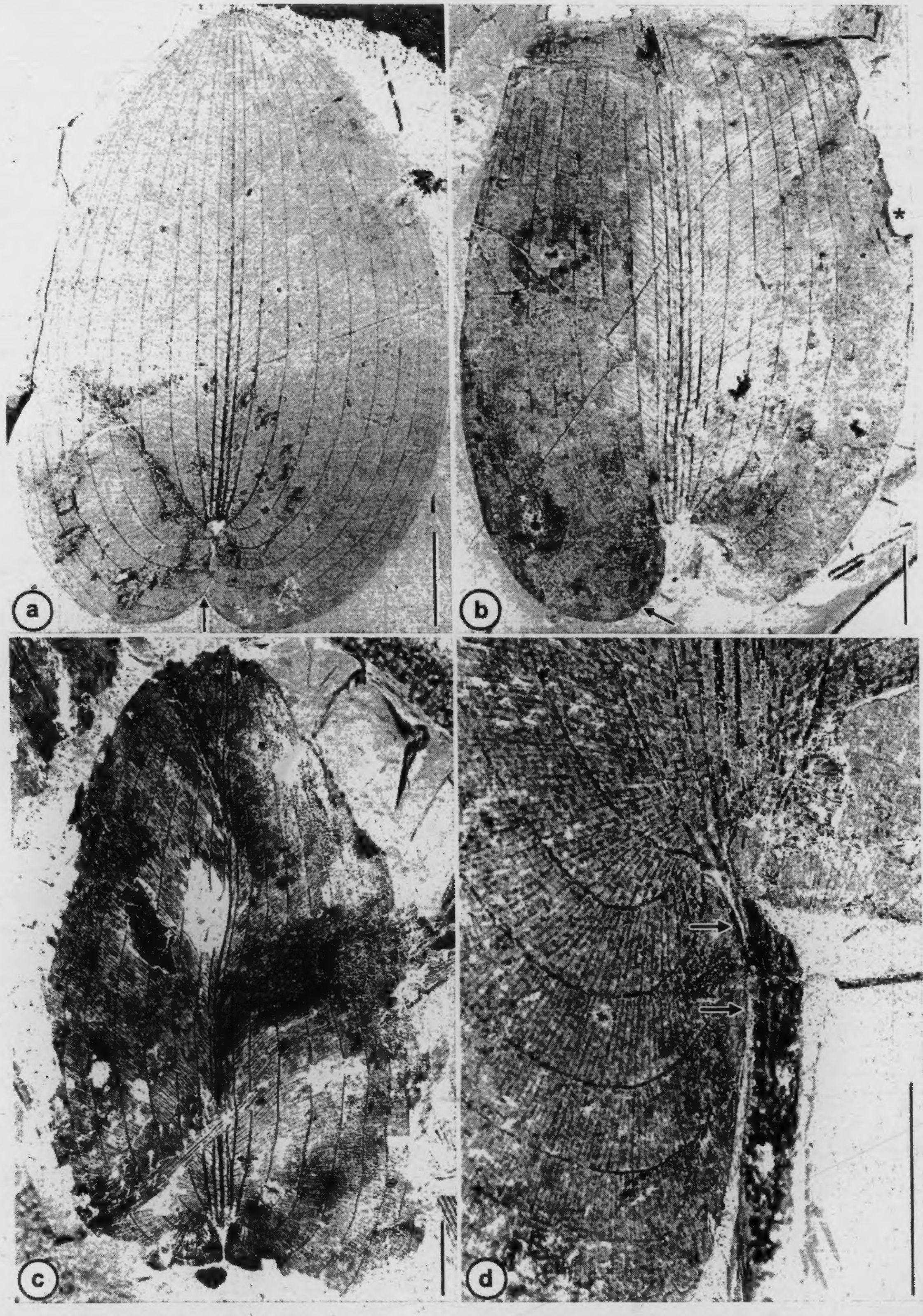

Figure 3.3

Figure. 3.3a-3.3i. *Cardstonia tolmanii* Riley et Stockey leaves.

Figure 3.3a. Lamina showing convex to rounded leaf apex. Scale bar = 5 mm. S52268A.

Figure 3.3b. Apex showing primary veins converging at what appears to be dark apical gland. Note primary veins occasionally anastomosing with adjacent primary near apex (arrow), but absence of primary veins merging with marginal vein. Scale bar = 2 mm. S52266A.

Figure 3.3c. Middle laminar area showing triple midvein, angle of divergence of secondary veins and finely preserved internal tissue (arrow), possibly aerenchyma. Note increase in number of secondary veins per cm toward margin. Scale bar = 1 mm. S52263A.

Figure 3.3d. Leaf margin showing secondary veins that anastomose and dichotomize (arrows), appear to alternate irregularly between major and minor veins, and that run perpendicular to the primary veins. Note marginal vein. Scale bar = 1 mm. S52272.

Figure 3.3e. Base of leaf (fig. 2c) showing triple midvein and apparent palmate radiation of primary veins (arrows). Scale bar = 1 mm. S50947A.

Figure 3.3f. Venation from fig. 3c showing alternation between major and minor secondary veins. Major veins can be either opposite or alternate between primaries. Note irregular branching pattern of tertiary veins (arrows). Scale bar = 1 mm. S52263A.

Figure 3.3g. Venation showing anastomosing and dichotomizing of major and minor veins. Note rare square shaped areole (arrow). Scale bar = 1 mm. S52263A.

Figure 3.3h. Venation showing extensive anastomosing and dichotomizing of primarily minor veins. Note tertiary veins crossing between adjacent secondary veins (arrows). Scale bar = 1 mm. S50989.

Figure 3.3i. Possible aerenchyma . Note several lacunae appear to overlap secondary veins (arrows). Scale bar = 0.5 mm. S52263A.

Figure 3.3

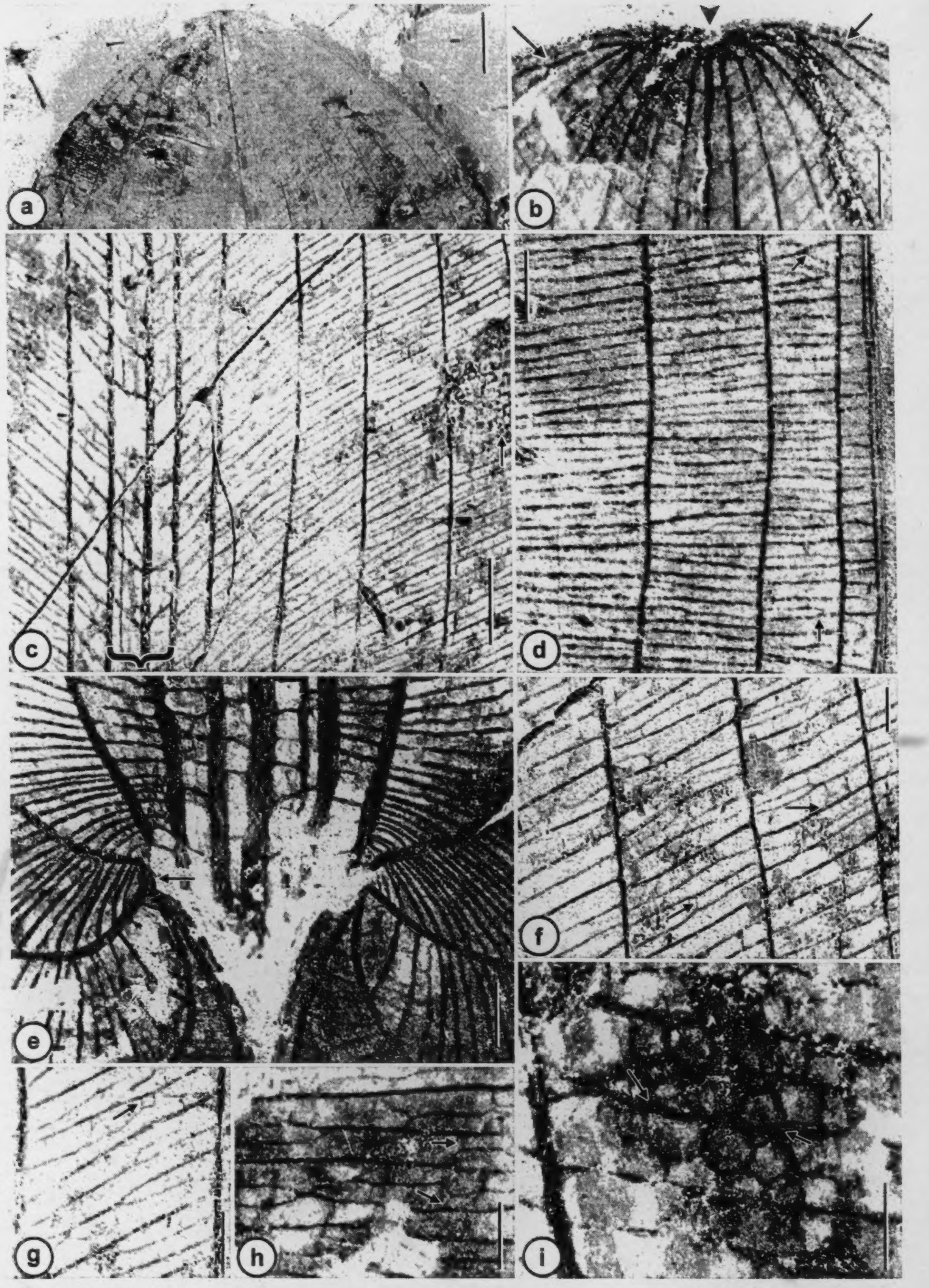

Figure 3.4

Figure 3.4a-3.4e. *Haemanthophyllum kamtschaticum* Budantsev.

Figure 3.4a. *H. kamtschaticum*, generitype, leaf fragment showing cordate base, recurved primary veins, dense secondary veins, and marginal vein (arrow). Scale bar = 0.5 cm. 960-1/2091 BIN RAS.

Figure 3.4b. *H. kamtschaticum*, generitype, enlarged lamina from fig. 4a showing secondary veins dichotomizing and anastomosing. Scale bar = 1 mm. 960-1/2091 BIN RAS.

Figure 3.4c. "*H. kamtschaticum*" leaf fragment showing long thickened petiole, cordate base and large laminar size. Scale bar = 3 cm. 960-1/2092 BIN RAS.

Figure 3.4d. *H. kamtschaticum,* generitype, lamina from fig. 4a enlarged to show secondary vein density and marginal vein. Scale bar = 2 mm. 960-1/2091 BIN RAS.

Figure 3.4e. *Haemanthophyllum* sp. (from type locality) lamina showing areolae. Scale bar = 1 mm. 960-1/3017 BIN RAS.

Figure 3.4f-3.4h. *Haemanthophyllum cordatum* Golovneva leaves.

Figure 3.4f. *H. cordatum,* holotype, lamina showing rounded apex and single lobe of cordate base. Scale bar = 2 cm. 967A/101 BIN RAS.

Figure 3.4g. *H. cordatum* leaf apex from fig. 4f. Scale bar = 0.5 cm. 967A/101 BIN RAS.

Figure 3.4h. *H. cordatum* leaf base from fig. 4f showing triple midvein (), recurved primary veins, and angle of divergence of secondary veins. Note radiating primary veins near petiole attachment (arrow). Scale bar = 0.5 cm. 967A/101 BIN RAS.

Figure 3.4

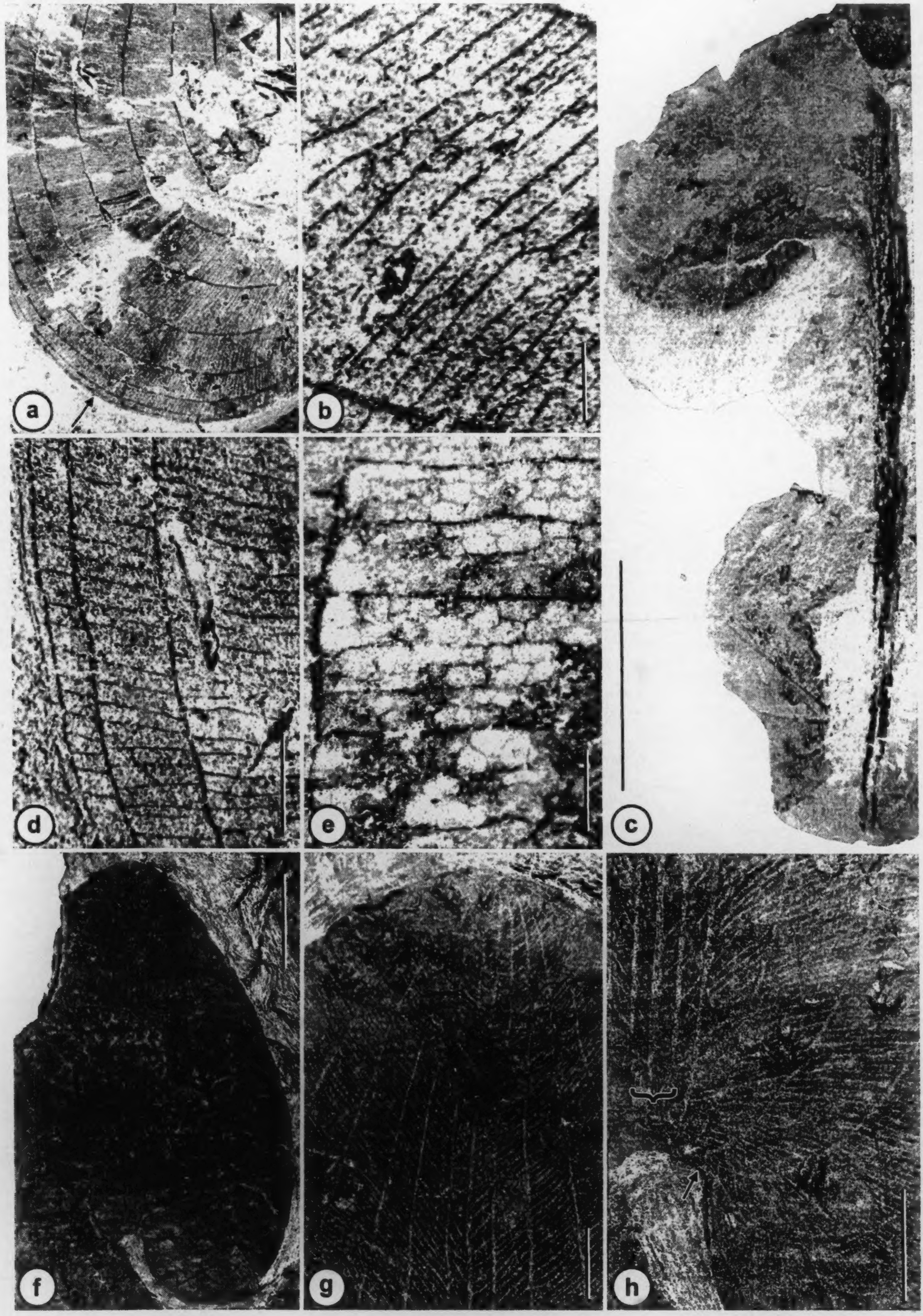

Figure 3.5

Figure 3.5a-3.5h. Selected extant taxa of Alismatales.

Figure 3.5a. *Echinodorus glaucus* Rataj leaf showing round apex, cordate base, recurved primary veins in base, and secondary veins nearly perpendicular at center. Note outer primary veins merge with margin before reaching apex (arrows). Scale bar = 3 cm.

Figure 3.5b. *Echinodorus grandiflorus*, abaxial surface, lamina showing many linear secondary veins (x) and fewer irregular sinusoidal secondary veins (o). Note numerous linear and branched tertiary veins running perdendicular to and terminating in adjacent secondary veins. Scale bar = 5 mm.

Figure 3.5c. *Caldesia* sp., leaf showing convex apex, deeply cordate base, recurved primary veins. Note outer primary veins merging with marginal vein subapically (arrow). Scale bar = 1 cm.

Figure 3.5d. *Caldesia* sp., leaf showing major (x) and minor (0) secondary veins. Note dichotomizing of major secondary veins (arrow). Scale bar = 1 mm.

Figure 3.5e. *Hydrocleys martii* Seubert, leaf showing rounded apex, cordate base, and recurved primary veins terminating in an apical gland. Note adjacent primary veins anastomosing (arrow); primary veins do not merge with marginal vein. Scale bar = 5 mm.

Figure 3.5f. *Hydrocleys martii,* abaxial surface of leaf base showing triple midvein and angle of divergence of secondary veins. Note numerous tertiary veins forming distinct areoles. Scale bar = 2 mm.

Figure 3.5g. *Limnocharis flava* (L.) Buchenau, abaxial surface of leaf showing rounded apex, cordate base, and recurved primary veins terminating in an apical gland. Note triple midvein in base of leaf. Scale bar = 4 cm.

Figure 3.5h. *Limnocharis flava*, abaxial surface, lamina showing major (x) and minor (o) secondary veins branching, and irregular branching of tertiary veins. Scale bar = 3 mm.

Figure 3.5

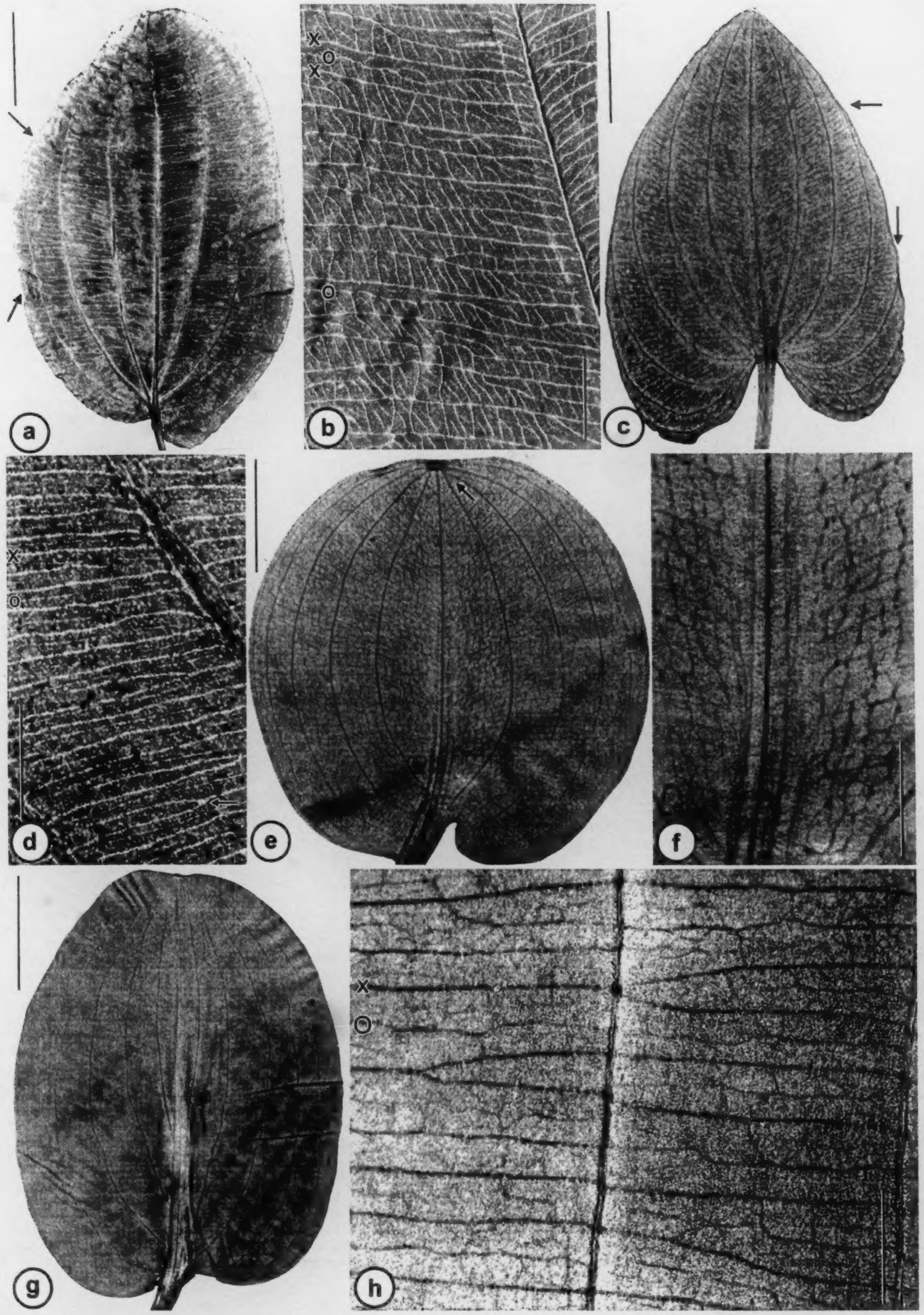
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Figure 3.6

Figure 3.6. Leaves of Alismatales.

Figure 3.6a. *Limnocharis laforestii* Duchessaing, whole leaf. Scale bar = 2 cm.

Figure 3.6b. *Limnocharis laforestii*, adaxial surface of leaf base showing triple mid-vein and random reticulate tertiary veins (arrow). Scale bar = 5 mm.

Figure 3.6c. *Limnocharis laforestii*, leaf apex showing primary veins merging near apex (arrow) and major (x) and minor (o) secondary veins. Scale bar = 1 cm.

Figure 3.6d. *Limnocharis laforestii*, abaxial leaf surface showing abaxial tertiary veins (arrowheads) that are slightly darker than abaxial tertiary veins. Note freely ending veinlets (4° veins) on adaxial side (arrow) and marginal vein. Scale bar = 2 mm.

Figure 3.6e. *Butomopsis latifolia* (D. Don) Kunth, whole leaf. Scale bar = 3 cm. DNA 1759.

Figure 3.6f. *Butomopsis latifolia*, adaxial leaf surface showing secondary veins (arrow) and tertiary veins with vertical elongate areoles over midvein (arrowhead). Scale bar = 3 mm. DNA 23463.

Figure 3.6g. *Butomopsis latifolia*, adaxial leaf apex showing primary and secondary vein patterns Scale bar = 5 mm. DNA 23463.

Figure 3.6h. *Butomopsis latifolia*, leaf margin showing major and minor secondary veins and tertiary veins with horizontally elongate areoles. Note marginal vein. Scale bar = 2 mm. DNA 23463.

Figure 3.6

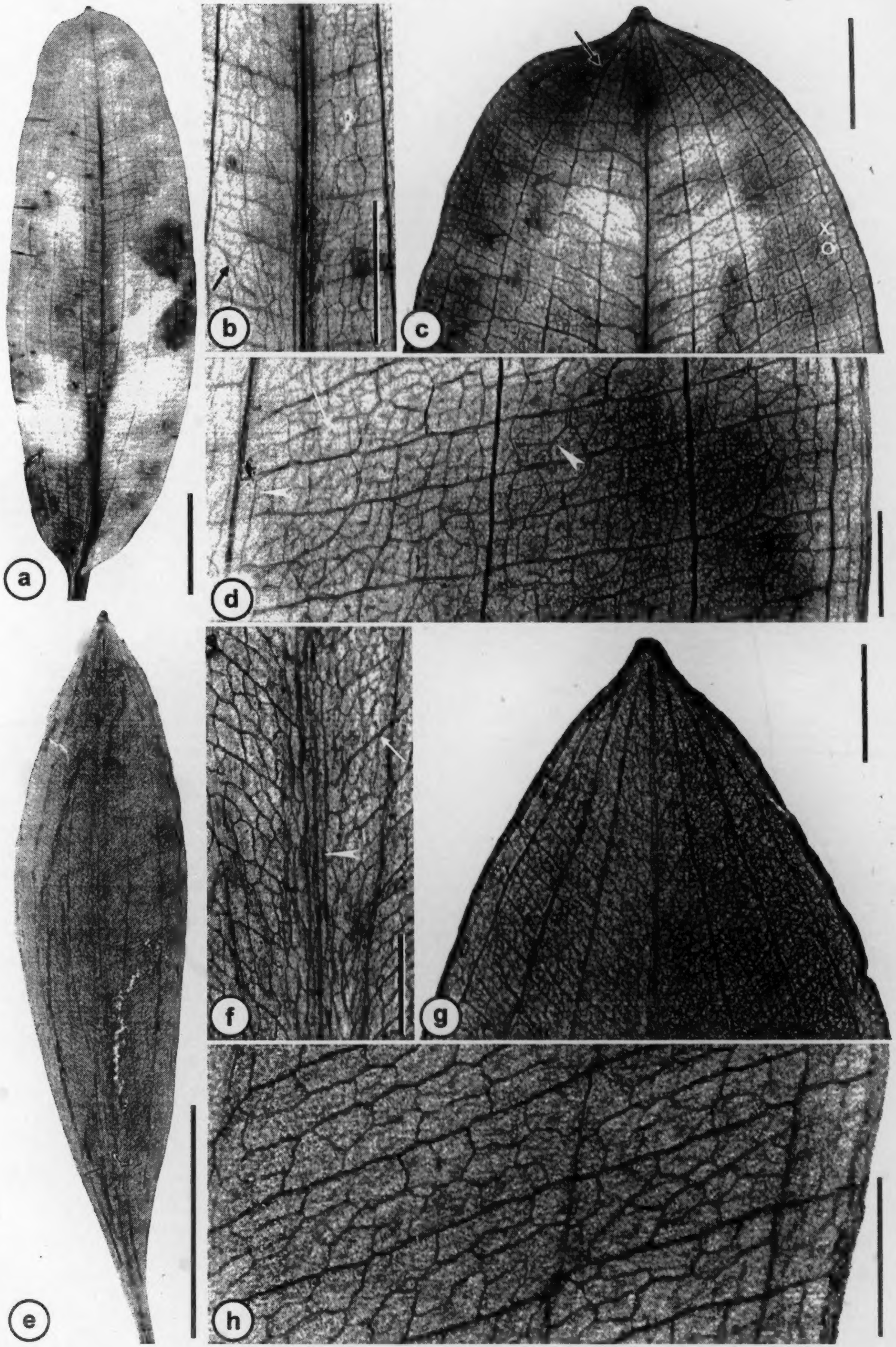

Table 3.1

Comparative morphology of *Haemanthophyllum* Budantsev species

Species	Locality	Age	Length (cm)	Width (cm)	Blade	Base	Apex	NLV	NCV
Haemanthophyllum zhilinii (Pneva) Golovneva	Kazakhstan	Late Oligocene-Early Miocene	20-40	~11	elliptical	cuneate	acuminate	11-13	10-20
Haemanthophyllum kamtschaticum Budantsev (**Generitype**)	Russia, Kamchatka Province	Late Paleocene/Eocene	?	7.5*	?	cordate	?	~ 21	**(24-35)**
Haemanthophyllum kamtschaticum Budantsev (original description)	Russia, Kamchatka Province	Late Paleocene/Eocene	12-35	7-17	broadly elliptical	cordate	attenuate to acuminate	17-21	9-13
Haemanthophyllum sp. 1	Russia, Amur Province	Paleocene	5	2	elliptical	cuneate	?	15	14-17 **(25)**
Haemanthophyllum sp. 2	Northern Ireland, County Antrim	Paleocene-Eocene boundary	?	2.2-2.8	oblong	?	?	13 **(17)**	6-8
Haemanthophyllum nordenskioldii (Heer) Boulter et Kvacek	Norway, Spitsbergen	Early Paleocene and Eocene	7-20	4-10	elliptical to ovate	cuneate to rounded	rounded to attenuate	15-21	7-9 **(14)**
Haemanthophyllum sp. 3	USA, North & South Dakota	Paleocene	~30	~15	broadly elliptical	?	acuminate	25	9-12
Haemanthophyllum sp. 4	USA, Alaska	Paleocene	~11	~5	ovate	rounded to cuneate	rounded	17-25	?
Haemanthophyllum sp. 5	Canada, Saskatchewan	Early Paleocene	~12	~7	?	?	acuminate	27	15-17
Haemanthophyllum cordatum Golovneva	Russia, Koryak Highlands	Late Cretaceous- Early Paleocene	4-18	3-14	ovate	cordate	rounded	**(13)**17-25	13-18 **(7-25)**
Cardston fossil	Canada, Alberta	Late Cretaceous	5-12	3.5-8.5	ovate	deeply cordate	convex to rounded	23-27	10-40

Note. NLV = number of longitudinal veins (1° veins) does not include the fimbrial (marginal) vein; NCV = number of cross veins (2° veins) per cm; * = estimate of leaf width; (boldface) difference in observed number of veins; table modified from Golovneva (1997).

Table 3.2

Comparison of morphological characters of *Cardstonia tolmanii* with selected extant taxa

Taxon	Family	Leaf Shape			# 1° veins	1° veins merge w/ fimbrial vein	1° veins merge w/ other 1° veins	# 2° veins per cm	Angle of divergence of 2° veins		Major & minor 2° veins	2° veins anastomose	2° veins dichotomize	3° veins present
		Blade	Base	Apex					Centre	Margin				
Cardstonia tolmanii Riley et Stockey		ovate to elliptic	cordate	convex to rounded	23-27	N	Y	10-40	45-60	90	Y	Y	Y	Y
Alisma subcordatum Raf.	Alismataceae[1]	obovate to elliptic	decurrent	convex	9	Y	N	5-12	35-45	70-90	N	N	Y	Y
Caldesia Parl. sp.	Alismataceae[1]	ovate	cordate	acuminate	13-15	Y	N	30	60	90	Y	Y	Y	N
Echinodorus glaucus Rataj	Alismataceae[1]	ovate to oblong	cordate	convex to rounded	11-12	Y	N	6-10	70-80	90	Y	Y	Y	Y*
Echinodorus grandiflorus (Chamisso et Schlechtendal) Micheli	Alismataceae[1]	ovate	cordate	convex	15	Y	N	8-11	60	90	Y	Y	Y	Y*
Echinodorus subalatus (Mart.) Griseb	Alismataceae[1]	ovate	convex	straight to convex	9	Y	N	8-9	50-55	50-55	Y	Y	Y	Y*
Aponogeton madagascariensis L. f.	Aponogetonaceae[1]	oblong	decurrent	emarginate	13	N	Y	5-6	80-90	80-90	N	N	N	N
Ottelia ulvifolia (Planch.) Walp.	Hydrocharitaceae[1]	oblong	cuneate	straight	7-19	Y	N	3-4	60-90	60-90	Y	Y+	Y+	Y*
Butomopsis latifolia (D. Don) Kunth	Limnocharitaceae[1]	elliptical	cuneate	straight to acuminate	7-9	N	Y	10-12	40-50	80-85	Y	Y	Y	Y
Hydrocleys martii Seubert	Limnocharitaceae[1]	elliptical	cordate	rounded	11	N	Y+	6-20	70	90	Y	Y	Y	Y
Limnocharis flava (L.) Buchenau	Limnocharitaceae[1]	elliptical	cordate	rounded	11-13	N	Y	11-13	60-80	90	Y	Y	Y	Y
Limnocharis laforestii Duchessaing	Limnocharitaceae[1]	oblong	cuneate	acuminate	11-13	N	Y	8-11	65-75	75-90	Y	Y	Y	Y*
Potamogeton lucens L.	Potamogetonaceae[1]	elliptic	decurrent	acuminate to convex	9	N	Y	6-10	40-60	60-80	N	Y	Y	Y
Haemanthus katherinae Baker	Amaryllidaceae[2]	oblong	cuneate	acuminate	21	N	Y	11-23	60	80	Y+	Y	Y	Y+
Stemona tuberosa Lour.	Stemonaceae[3]	ovate	cordate	acuminate	11	N**	N	28-30	90	90	Y	Y	Y	N

Note: # 1° Veins = number of primary veins in total (not including fimbrial); # 2° veins per cm = number of secondary veins (both major and minor) per cm; * = fourth order venation; ** = no fimbrial vein present; + = rare occurrence; Orders (APG 1998): [1]Alismatales, [2]Asparagales, [3]Pandanales.

Chapter 4

Conclusions

The St. Mary River Spillway locality from the Late Cretaceous of southwestern Alberta has yielded an extremely well-preserved fossil megaflora composed primarily of aquatic plants inhabiting shallow lakes and ponds. Rapid deposition in siltstones and fine-grained sandstones during overbank flooding has preserved many of the aquatic plants from this ancient community *in situ.* This has enabled whole plant reconstruction of two new species from this locality to date, the description of a new broad-leaved monocot (Chapter 3) and the possibility of reconstruction of several unidentified herbaceous monocots and "dicots". An improved understanding of these ancient aquatic communities has also resulted from the interpretation of the depositional environments.

Palynological samples from the spillway are currently the primary constraint on the age of the locality and also in the formation as a whole. Very little work has been done to date on dating or correlating the St. Mary River Formation to coeval strata, so any data available should improve our understanding of these strata. Currently, radiometric dating on an ash layer collected from the locality is underway. The possibility of magnetostratigraphic dating is also possible from drill cores. Establishing an accurate age is particularly important if a comparison with floras of similar age is undertaken.

The depositional environment is interpreted as an anastomosed fluvial system with numerous shallow lakes and ponds. Seasonal flooding played a major role in shaping the local environment with the floodplain being frequently inundated with high clastic input. This rapidly buried the surrounding plant communities, causing repeated interruption of soil formation and rapid habitat alteration. Plants may have had to evolve growth strategies to overcome sudden burial.

The St. Mary River Formation has been characterized as a semi-arid environment, but this study showed no indication at the primary excavation sites or in the palynological samples of aridity. However, caliche zones were noted both up-section and down-section from the study sites, with some indication from palynology that arid environments might have occurred. This suggests the period of time in which the sediments at the primary excavation site were deposited was wetter than normal and the location was possibly a local lowland or basin. However, further sedimentological and floristic studies are needed to confirm this observation and to understand climate change better over the depositional history of the formation.

The co-occurrence of taxodiaceous foliage and palms, and the proximity of the Bearpaw Sea, may indicate a warm, humid climate. Leaf Margin Analysis appears to corroborate warmer mean annual temperatures, although estimates could be greatly improved by an increase in the number of "dicot" species sampled. Therefore, further collections from various depositional settings and strata should be made to improve species counts and also remove margin biases associated with local habitats and riparian settings. This should improve local temperature estimates and provide a better understanding of possible climatic changes over time.

Future studies on the St. Mary River Spillway locality are required to understand and document the floristic diversity, climate, and microenvironments that existed. This flora should then be compared to fossil localities known from the Little Bow, Oldman and Belly Rivers to provide a more comprehensive picture of the plant fossil assemblages that existed both spatially and temporally throughout the St. Mary River Formation. In addition, floras of similar age to the St. Mary River Formation are known from the Horseshoe Canyon Formation of southern Alberta, the Meeteetse Formation of northern Wyoming, the Fruitland-Kirtland Formations of New Mexico, and the Rarytkin Formation of northeastern Russia. A potential project comparing the regional climate, ecosystems, taxonomic relationships, and diversification patterns could increase our understanding of Northern Hemisphere plant communities at a critical time in vegetational turnover during the Late Cretaceous.

In this study, *Cardstonia tolmanii*, a new genus and species of aquatic, broad-leaved monocot is described, with possible affinities to extant Limnocharitaceae (Alismatales) . Leaf shape, venation pattern and areolation of *C. tolmanii* are compared to that in living and fossil monocots and to fossil leaves described as *Haemanthophyllum* Budantsev from northeastern Russia. In addition to *C. tolmanii*, at least three other taxa of broad-leaved monocots are present at the St. Mary River Spillway locality. However, during the study of *C. tolmanii*, it became readily apparent that using keys and terminology for "dicot" leaves to describe broad-leaved monocots was of limited value. This suggests that a separate morphological description and categorization for monocot leaf architecture be undertaken, which should improve our understanding of extant monocot venation patterns, and provide a better terminology with which to describe them properly.

The rarity of broad-leaved monocots in the fossil record in general, especially from the Cretaceous, makes this locality particularly important in documenting the early diversification of this group. Furthermore, the possibility of whole plant reconstructions of two aquatic plants - a large, double-toothed, rosette-forming "dicot" and an herbaceous, chloranthoid-toothed, long-petiolate, net-veined "dicot" are possible due to rapid *in situ* preservation.

Preservation is remarkable at the St. Mary River Spillway fossil locality with cuticular remains, epidermal cell patterns, and internal anatomy present in some specimens. This level of surficial and anatomical detail, combined with the large numbers of aquatic plants preserved *in situ*, will continue to make this locality extremely important in the study of whole plants, and in reconstructing these Late Cretaceous plant communities. Continuing studies on the collected material and further excavations at the St. Mary River Spillway should improve our understanding of species diversity, paleoclimate, and depositional environments.

Appendix A

Palynoflora

Department of Natural Resources Canada

Geological Survey of Canada

Paleontological Report 6-ARS-1999

A. R. Sweet

Paleontology Subdivision

Institute of Sedimentary and Petroleum Geology

Appendix A

Geological Survey of Canada Paleontological Report 6-ARS-1999

Applied research report on seven samples of latest Campanian or early Maastrichtian age from the St. Mary River Formation, St. Mary River Dam spillway (NTS82H/6; Zone 12U, 347300 m E, 5470600 m N), southwestern Alberta as requested by Mike Riley and Georgia Hoffman (Biological Sciences, University of Alberta, Edmonton, Alberta).

The relevant parts of any manuscript prepared for publication that paraphrase or quote from this report should be referred to the Paleontology Subdivision, Calgary for possible revision.

Sample P4454-1; C-401368; 33.3 m horizontally from datum, dark grey mudstone with shell debris.

Selected flora: See Table A.

Comments: Recovery sparse, preservation poor to average. Residue dominated by cuticular debris.

Depositional environment: The presence of abundant *Sigmopollis* is taken to indicate a fluvial influence.

Age: Based on the recovered assemblage the age is within the range of latest Campanian to early Maastrichtian with the greatest constraints provided by the presence of *Aquilapollenites augustus* and *A. drumhellerensis*.

Sample P4454-2; C-401369; 81 m horizontally from datum, greenish-grey mudstone.

Selected flora: See Table A.

Comments: Recovery sparse to good, preservation average to good. Residue dominated by angiosperm pollen and in particular *Sparganiaceaepollenites* with fusinite being the dominant organic debris.

Depositional environment: The dominance of the assemblage by *Sparganiaceaepollenites* together with the presence of *Penetetrapites* is taken to indicate a near shore lacustrine depositional environment.

Age: Based on the recovered assemblage, only an unconstrained late Campanian to Maastrichtian age is indicated.

Sample P4454-3; C-401370; 153 m horizontally from datum, dark grey organic-rich mudstone.

Selected flora: See Table A.

Comments: Recovery and preservation average. Residue dominated by terrestrial palynomorphs and vascular debris.

Depositional environment: The near dominance of Sigmopollis is taken to indicate a fluvial influence.

Age: Based on the recovered assemblage only an unconstrained late Campanian to Maastrichtian age is indicated.

Sample P4454-4; C-401374; 450 m horizontally from datum, dark grey mudstone with scattered shell debris and sandstone interbeds.

Selected flora:

Cyathidites sp. (scarce)

Laevigatosporites sp. (scarce)

Sigmopollis sp. (scarce)

Comments: Recovery very spare, preservation average. Residue dominated by fusinite and probable amber microdroplets.

Depositional environment: The concentration of fusinite and amber suggests an oxidizing depositional environment. The presence of shell debris indicates a backwater fluvial or lacustrine setting.

Age: Indeterminate.

Sample P4454-5; C-401375; 460 m horizontally from datum, dark grey mudstone with abundant shell debris.

Selected flora:

Cyathidites sp. (common)

Laevigatosporites sp. (common)

Sigmopollis sp. (scarce)

Zilvisporis sp. (rare; bryophyte spore)

Comments: Recovery sparse. Otherwise as for C-401374.

Depositional environment: As for C-401374.

Age: Indeterminate.

Sample P4454-6; C-401376; 550 m horizontally from datum, greenish-grey, hackly, silty mudstone.

Selected flora:

Concentricystes sp. (scarce)

Cyathidites sp. (common)

Laevigatosporites sp. (common)

Comments: Recovery very sparse, preservation poor. The small organic residue that was recovered is dominated by fine fusinitic debris.

Depositional environment: This style of preservation and the assemblage, especially the presence of *Concentricystes*, is similar to that found in the "semi-arid" caliche-rich paleosoils of the Willow Creek and Porcupine Hills formations. This implies the sampled site part of a well drained, possibly seasonally dry depositional setting.

Age: Indeterminate.

Sample P4454-7; C-401377; 700 m horizontally from datum, medium grey shale with abundant plant debris.

Selected flora: See Table A.

Comments: Recovery and preservation good. Residue dominated by terrestrial palynomorphs and vascular debris.

Depositional environment: The dominance of *Laevigatosporites* combined with an abundance of T/C/T (Taxodiaceae/Cupressaceae/Taxaceae) pollen is suggestive of a swamp or swamp-margin depositional setting. The common presence of microsporangial clumps of *Laevigatosporites* indicates deposition at or close to the growth site of the parent plant.

Age: Based on the recovered assemblage only an unconstrained late Campanian to Maastrichtian age is indicated.

GENERAL COMMENTS

The lack of age-specific angiosperm pollen limits the biostratigraphic usefulness of the recovered assemblages. Sample C-401368 contains the most age specific assemblage but still one that does not allow the definition of a closely constrained age.

Each of the three samples that were counted (Table 1) differs in the dominant taxa present and hence express differences in the local ecological niches present.

From previous studies an association has been made between the presence of the algal spore *Sigmopollis* and a strong fluvial influence on the site of deposition. The darker grey mudstones of C-401368 and C-401370 yielded the highest numbers of *Sigmopollis* and hence the inference of a fluvial influence.

The presence of *Concentricystes* sp. is indicative of a better drained depositional environment than that of the other samples.

The microsporangial clumps of *Laevigatosporites* in sample C-401377 indicates a close association with the site of growth of the parent plant.

The following affinities are suggested:

1) The monosulcate pollen referred to as *Cycadopites* may be allied may be allied to either *Cycad* or *Gingko*;

2) *Laevigatosporites* sp. in samples 1 and 3 could be the exinous wall of a

Dryopteridaceae (e.g., *Onoclea*) fern, but this is one of many possible affinities;

3) *Lygodium* sp. is allied with, *Lygodium*;
4) *Arecipites microreticulatus* has been considered allied to Palmae but there are other possible affinities;
5) *Cranwellia* has affinities with Loranthaceous pollen;
6) *Fraxinoipollenities* has been considered to be pollen from *Platanus;*
7) *Liliacidites* is allied with Liliaceae but there are other possibilities;
8) *Sparganiaceaepollenites* is closely similar to pollen of *Sparganium* but may also represent monads of *Typha*; and
9) *Ulmoideipites* sp. is ancestral to the Ulmaceae.

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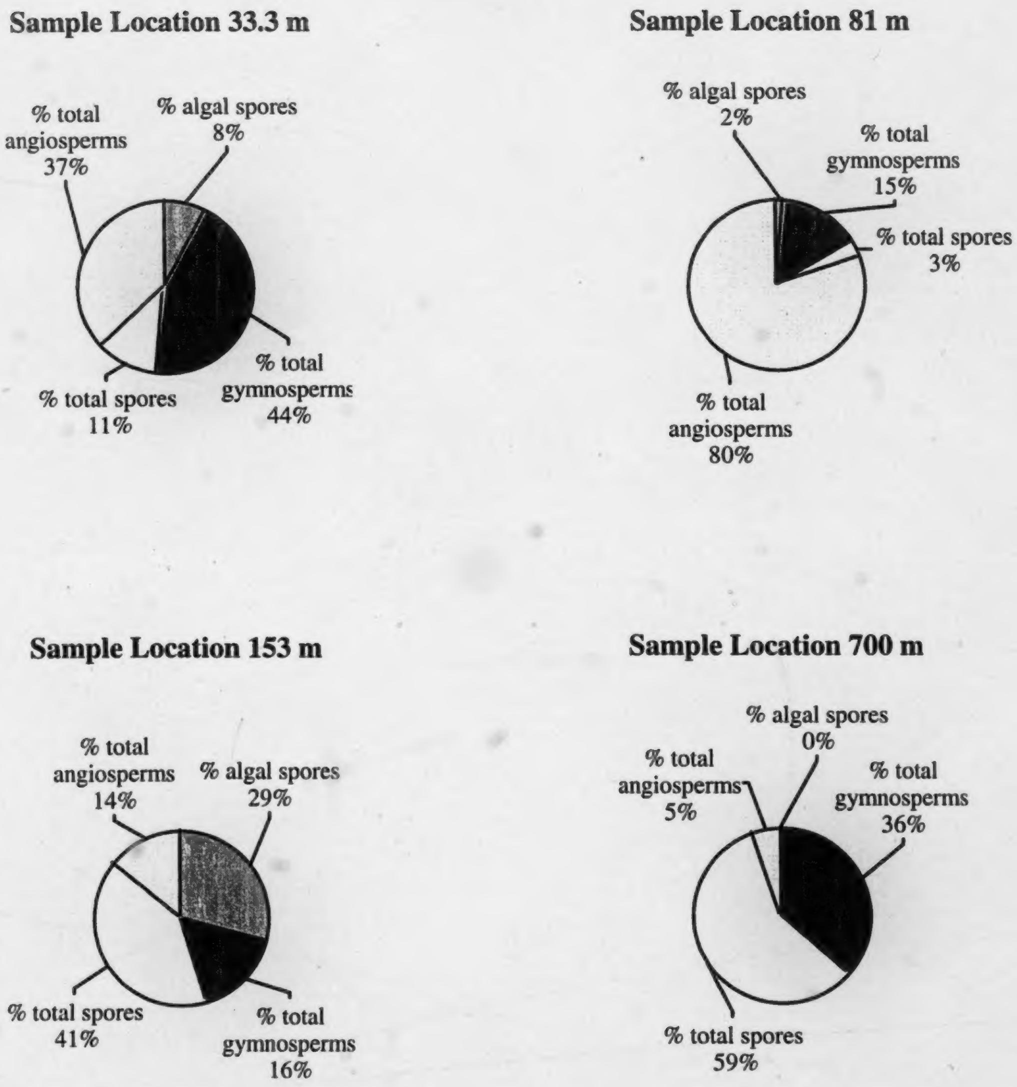
Table A

St. Mary River Spillway: Palynology for Selected Sample Sites				
C-number	401368	401369	401370	401377
P-number	4454-1	4454-2	4454-3	4453-7
Sample location	33.3 m	81 m	153 m	700 m
Algal spores				
Sigmopollis sp.	14	4	63	
Other algae (*Schizophacus*)	R	R		
Total algal spores	14	4	63	0
Gymnosperms				
Taxodiaceae/Cupressaceae/Taxaceae (T/C/T)	72	25	31	84
bisaccate pollen	2	5	2	4
Cycadopites sp. (*Ginkgo* ?)	2	3	1	
Total gymnosperms	76	33	34	88
Spores				
Laevigatosporites sp.	14	3	31	133
Cyathidites sp.	5	3	53	8
Osmundacidites sp.			1	
Zilvisporis sp. (*Riccia-* type)			1	
Glecheniidites sp.			1	
Lygodium sp.		A		
Total spores	19	6	87	141
Angiosperms				
Aquilapollenites attenuatus Funkhouser 1961		R		
A. augustus Srivastava 1969	R			
A. drumhellerensis Srivastava 1969	R			
A. quadrilobus Rouse 1957		C		3
Arecipites microreticulatus Anderson 1960	11	5		
betulaceous-type			1	3
Cranwellia rumseyensis Srivastava 1966	20	1		
Dyadonapites reticulatus Tschudy 1973	2	2	2	
Fraxinoipollenites sp.	1	7	6	3
Liliacidites complexus (Stanley) Leffingwell 1971	1		4	1
Liliacidites spp.	3		4	
other tricolpate pollen	9	10	11	2
Pandaniidites sp.			R	
Penetetrapites inconspicuus Sweet 1986		5		
Retimonocolpites sp.	2	R		
Simplicepollis rallus (Stanley) Nichols & Brown 1992	R			
Sparganiaceaepollenites sp.	3	142	2	1
Subtriporopollenites alpinus (Wolf) Tschudy 1973	10	2		
Triatriopollenites costatus Norton in Norton & Hall 1969	R			
Triporopollenites plektosus Anderson 1961	2	4		
Ulmoideipites sp.				2
Total angiosperms	64	178	30	13
TOTAL COUNT	173	221	214	242
R = 1 to 2; S = 3 to 5; C = 6to 8; A = more than 8 specimens seen outside count area				
Percentages				
% algal spores	8.1	1.8	29.4	0.0
%T/C/T pollen	41.6	11.3	14.5	34.7
%other gymnosperm pollen	2.3	3.6	1.4	1.7
% total gymnosperms	43.9	14.9	15.9	36.4
% *Laevigatosporites*	8.1	1.4	14.5	55.0
% *Cyathidites*	2.9	1.4	24.8	3.3
% total spores	11.0	2.7	40.7	58.3
% total angiosperms	37.0	80.5	14.0	5.4

Appendix B



Sample Location 33.3 m

Sample Location 81 m

Sample Location 153 m

Sample Location 700 m

Figure B.1. Pie diagrams presenting relative abundance of miospores recovered from four samples from St. Mary River Spillway fossil locality. Miospore counts used in calculating relative percentage of each taxonomic group are taken from Geological Survey of Canada Report 6-ARS-1999 produced by Art Sweet (Appendix A).

Appendix C

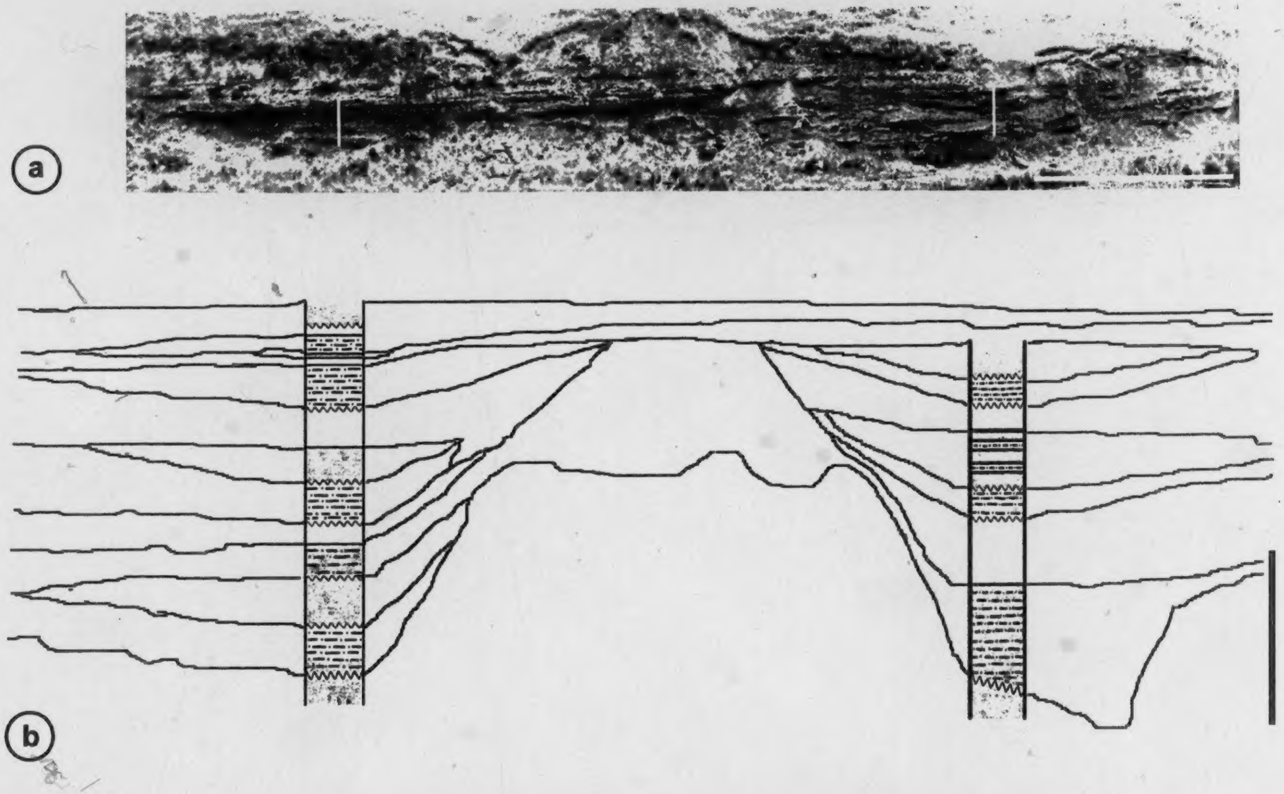


Figure C.1. **a**), Photomosaic of site 2 showing position of two measured sections (vertical lines). Scale bar (horizontal line) = 20 m. **b**), Correlation of exposed beds relative to measured sections. See List of Symbols and Abbreviations for lithological symbols. Scale bar = 1 m.

Appendix D

Leaf Margin Analysis Calculations

Leaf-estimated Mean Annual Temperature [(L)MAT] equation using Wolfe (1979) data set (Wing and Greenwood, 1993):

$(L)MAT = 30.6 * P + 1.14$

P = proportion of woody dicotyledonous species with entire-margined leaves

sample of 13 taxa: toothed margin = 8; entire margin = 5 $\therefore$ $P = 5/13 = .39$

$(L)MAT$ $= 30.6*.39 + 1.14$ = **$13.1^{\circ}C$**

A small sample may bias the (L)MAT estimate introducing a sampling error so, a standard deviation calculation is used (Wilf, 1997):

$\sigma((L)MAT) = c[((P(1-P))/r]^{-2}$

c = slope of regression = 30.6

r = number of species

$\sigma = 30.6[(.39(1-.39))/13)^{-2} =$ **$\pm 4.1^{\circ}C$**

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To Whom it may concern,

Permission has been granted for Michael G. Riley to use Chapter 3 in his thesis: Paleobotany and Paleoecology of the St. Mary River Spillway Locality (Late Campanian/Early Maastrichtian), Cardston, Alberta.

Ruth A. Stockey,